ONE– OR TWO–DIMENSIONAL ACTION OF MUTANT LOCI?

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In a group of recent papers Curt Stern[1] analyzed genic action by studying the effects of a gene in different dosages, in different alleles and compounds and under different environmental conditions. It was believed impossible to explain the data which he obtained on the assumption of a single type of genic action. Stern, therefore, elaborated an ingenious though rather complicated scheme of genic action based on certain assumptions proposed by S. Wright. It is my intention to show that the factual data do not require such a complicated interpretation but fall, within expected limits, in line with formerly derived simpler assumptions.

A short summary of the decisive data in Stern's own words is:

In *Drosophila* the fourth chromosome gene cubitus interruptus (ci) is recessive to wild type (+) at 25° and slightly dominant at 14°. At both temperatures the effect of two doses of ci is more normal than that of one and less than that of three. Thus ci contributes towards normality. The normal allele alone, in a single dose, assures normality at 25° and not at 14°, where a slight ci effect appears. At 14° the heterozygote +/ci deviates more from normality than flies carrying the +-allele alone: the cumulative effect due to "addition" of ci to a genotype containing ci only, is reversed into an antagonistic effect if ci is added to the +-genotype. Possession of both negative and positive properties of the ci allele may be interpreted, following Wright, in terms of (1) power of the gene to combine with a limited cellular substrate (S) and (2) efficiency of the gene in converting S into a product involved in the formation of normality. The ci-allele appears lower in both combining power and efficiency than the +-allele.

To these basic facts Stern and Schaeffer later added more data. (1) Three different wild-type alleles (in

[1] C. Stern, *Genet.*, 28: 441–475, 1943. C. Stern and E. W. Schaeffer, *Proc. Nat. Acad. Sci.*, 29: 351–361 and 361–367, 1943.

Stern's interpretation) were found which acted differently in heterozygotes with ci. (2) The heterozygotes of these with a deficiency for ci (M_4) and the triplo-IV combinations of many viable combinations were added to the series. The results were explained again in terms of antagonistic effects based upon different gene-controlled reactions of the type just reported.

We begin with the three wild-type alleles which Stern calls $+^c$, $+^2$, $+^3$. If we call the interruption of the cubital vein in different degrees (Stern's classes 0–2) the ci effect, the first two "isoalleles" (Stern) have no effect at low temperature but $+^3$ has a slight ci effect, *i.e.*, a few ci individuals appear. Opposite a deficiency, however, all have a slight ci effect, which is largest for $+^3$ and intermediate for $+^2$. Though Stern describes these alleles as wild-type alleles we must not forget that in the usual terminology $+^3$ at least would be called a low ci-allele, just as vg^{ni} with no effect but a few nicked flies is called a vg-allele. This difference in terminology is of no importance in principle, for in such a case the limits between + and mutant alleles are arbitrary. But the issue might be confused if one does not realize that both sets of terms mean the same thing.

We turn now to the facts, *i.e.*, the phenotypes of different combinations, measured in ci classes N ($=+$) 0, 1, 2, of the alleles $+^c$, $+^2$, $+^3$, ci, Df ci (M_4), all in diploid and triploid (via triplo-IV) combinations. I have chosen to represent the facts graphically, using only a minimum of such assumptions without which genic action could not be described. We may assume that the effect of the loci is the production of vein-forming substance, whatever this may mean. (It would also be possible to work a reciprocal scheme with vein-preventing substance). We may also assume that the amount of this substance available at the time of determination of the cubitus is the consequence of a chain of reactions controlled by the loci in question. A definite amount surpasses the threshold above which the vein is normal; the abnormal classes are inversely proportional (*ceteris paribus, e.g.,* tempera-

ture, modifiers) to the amount of this substance below the
threshold for normality. I repeat that these are the
minimum assumptions without which no genic action can
be described in dynamic terms. Thus we can represent
Stern's data in the diagram Fig. 1 in terms of simple
genic actions. The lines representing the reaction-chains
of the different combinations studied by Stern are drawn
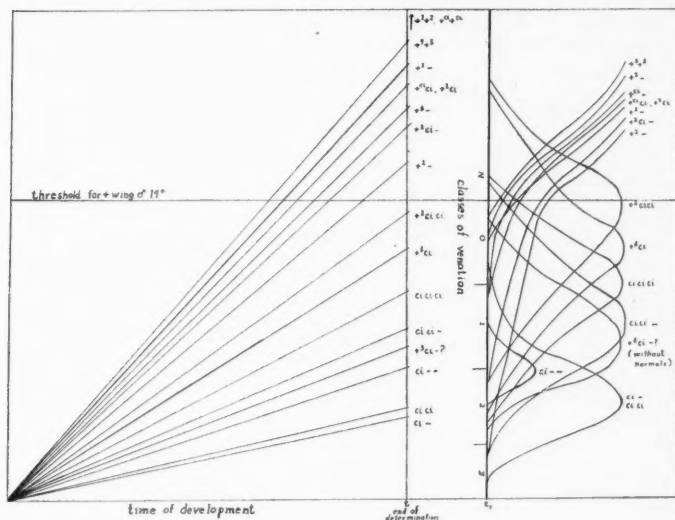so that they represent approximately (*i.e.*, by inspection

FIG. 1.

of his data, not by exact calculation) the means of the
effect. On the right of the figure actual variation as
registered in Stern's tables is drawn half diagrammati-
cally using his classification. This part of the diagram
is to be superimposed upon the main drawing with lines
t and t_1 being identical.

The basic data in this case as in many others require
the assumption that there is a threshold for the determin-
ing reaction above which the normal wild type is pro-
duced. Any number of hyperthreshold wild phenotypes
are imaginable, but they can be proven only if hemizygous
or in compounds or if temperature or other effects push
some individuals below the threshold. In these cases only

the subthreshold part of the curves of variation is known
(upper part of t_1), but the known part allows the alloca-
tion of the order of the means for hyperthreshold means.
Means below the threshold are supposed to correspond
to the means of the curves of variation of the effect and
the measure are Stern's classes 0–3 as marked on t_1. The
figure then represents the actual facts in terms of quanti-
ties of a single product of reaction.

Our problem is to find out whether these actual results
are consistent without making further assumptions. This
is identical with the question whether Stern's description
of the facts is indispensable, namely, that ci in presence
of ci only has a summative effect, adding towards nor-
mality, but in the presence of wild type has the opposite,
antagonistic effect, subtracting from normality. It is this
interpretation which requires, in Stern's view, a theory
of the type he developed (see the quoted papers for this
theory; not the theory itself but the need of its formula-
tion is under discussion here).

In order to derive expectations on the basis of the
simple description of genic actions in terms of quantities
of reaction products we must look for a basis of our evalu-
ation. The only visible one is found in the typical rela-
tions of multiple alleles. In the overwhelming number of
instances the phenotype of a compound is intermediate
between the two homozygotes, and therefore the action of
the alleles n^1, n^2 in the compound is $\dfrac{n^1 + n^2}{2}$. If the wild
type is completely dominant this may have the same
cause, *i.e.*, the curve of the heterozygote $+/n$ would be
above the threshold. If dominance were the result of
modifiers alone the system would still work in F_1. As in
the present case two wild-type alleles are known which
have subthreshold effects, (assuming Stern's terminol-
ogy) the situation for these is the same as if they were
lower multiple alleles of ci (which they are, in the usual
way of describing such facts). Thus we may assume that
the expectations for the phenotypes are always based
upon the simple formula $\dfrac{n^1 + n^2}{2}$. There is no reason to

expect a different effect in the case of one (deficiency) or of three (triplications) alleles, except for such actions based upon other loci involved, *i.e.*, within the deficiency or within the duplication (triplo IV). Thus a first approximation to our expectations for the phenotypes must be derived from the known differences of the homozygotes, using the formula $\dfrac{n^1 + n^2\,(+\,n^2)}{2}$ for the different combinations. We know in the present case the order of effects of $+^c$, $+^2$, $+^3$ homozygous and of ci ci. If we assume a value for the threshold of normalcy (mean) of 20 units of the determining principle we can assign the following mean estimated values: $+^c = 44$, $+^2 = 34$, $+^3 = 24$, assuming that the normal variation (at $25°$) does not transgress the threshold at 20; ci would have an action of 8 units. For the deficiency we do not have much information; its action value might be zero or a small value. We will assume a value of 2. Thus we can calculate the phenotypic expectation for all combinations in relation to the basic homozygous phenotypes and establish the expected order of phenotypes on the basis of effects of simple proportions. This has been done in Table 1, where the first three columns give the expected order and the fourth the actual order as found in Fig. 1. Curves which are near each other have been given the same number. It is needless to say that this procedure is a rather crude one. But as we have no way of knowing whether a small but statistically significant difference in the mean is exclusively due to the specific genic action, more refined methods are hardly needed.

Looking at the table we see that with only two or three major exceptions the results are roughly those expected on the basis of a simple genic action. In all the smaller discrepancies the deficiency is involved which is known to affect general developmental features. Only one combination falls completely out of the series, namely $+^2$ ci ci, where the two ci are largely dominant. But this result can not be derived from Stern's antagonistic actions either: his viewpoint would account for this as well as the

opposite result, if the latter would have been found (as it is found in a majority of triploid combinations of other loci). The No. 9 case with a shift out of order towards ci is hardly in agreement with Stern's interpretation except if a special assumption is made regarding the action of the deficiency. But this combination is not completely reliable (see footnote); in case No. 11, the third aberrant case, the deficiency acts in the opposite direction. I find difficulties in applying the same interpretation to both cases. Further Nos. 7–8 and 10–11 ought

TABLE 1

Expected order	Compound	Value $\frac{n^1 + n^2 (+ n)}{2}$	Actual order ♂ cold	Far off towards + or ci
1	+^{c} +^{c}	44	1	
2	+^{z} +^{z}	34	2	
3	+^{z} ci ci	25	8	! → ci
4	+^{z} +^{3}	24	3	
5	+^{c} – (– = DfM$_4$)	23	4	
6	+^{z} ci –	22	4	
7	+^{z} ci	21	5	
8	+^{z} –	18	5	
9	+^{3} ci –	17	8*	! → ci
10	+^{3} ci	16	7	
11	+^{3} –	13	6	! → +
12	ci ci ci	12	9	
13	ci ci –	9	10	
·14	ci ci	8	11	
15	ci – –	6	10	
16	ci –	5	12	

* This does not follow directly from Stern-Schaeffer's data in which the N-class could not be checked but is extrapolated from the trend of the curve in the observed classes.

to give parallel results on whatever assumption, but their order is in opposite directions. I am inclined to consider this as based on chance (which includes the action of deficiencies) rather than upon such differences between +^{c} and +^{3} which Stern must assume to explain the small discrepancy.

Looking over the entire assemblage of data I come to the conclusion that with one exception (+ ci ci) the facts do not require the assumption of two opposite effects of ci, whether alone or combined with plus. I wonder whether the small discrepancies from simple expectations require the complicated theory which is based upon the description of the data in terms of antagonistic effects. I wonder further whether in the majority of cases in

which the $+rr$ ($r =$ recessive) form is known to be of the wild type the dosage rule for rrr does not hold. I might finally venture the opinion that a simple explanation would not have appeared so difficult if Stern had not interpreted the dosage effects of the series ci, ci ci, ci ci ci as demonstrating that ci contributes something towards normal. This seems to me to be an unnecessary method of interpretation when the ''naive'' interpretation expressed in the formula $\dfrac{ci + ci + ci}{2}$, etc., describes the facts perfectly.

Speaking generally, then, the difference between our views is this: Stern attributes the decisive weight to such discrepancies within comparable pairs as the inverted order of effects in Nos. 10–11 or 9–11, discarding the possibility of specific influences of the deficiencies upon the normal rate of the underlying processes. I prefer to look at the general orderliness of the whole series and to attribute minor discrepancies to such specific features as the ontogenetic effects of deficiencies. The only really great discrepancy, No. 3 of Table 1, is the case in which considerable dominance of two recessives over one dominant is involved. I am inclined to consider this as a special phenomenon to be interpreted independently of the simple proportionality of actions of the other combinations. Here the problem of the ''covering or not covering'' of recessives by a duplication enters, which, I think, has not yet found a solution.

The reason why this criticism is offered is first that Stern's experiments are so excellently conceived and carried out that their interpretation is of paramount importance; second, that the present author strongly believes that simple explanations ought to be preferred as long as it can possibly be justified, because organic processes could never work if they were not basically simple. I am greatly indebted to my friend Professor Stern for reading the manuscript of this paper, stating his counter criticism and assenting to its publication.

CHROMOSOME STUDIES ON EIGHT SPECIES OF SCIARA (DIPTERA) WITH SPECIAL REFERENCE TO CHROMOSOME CHANGES OF EVOLUTIONARY SIGNIFICANCE[1]

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INTRODUCTION

WITH the rediscovery of the giant chromosomes in the larval salivary glands of the Diptera by Heitz and Bauer (1933) and their application to genetic research by Painter (1934), students of evolution were provided with a new and powerful tool for studying the problems of evolutionary chromosome changes. In *Drosophila*, numerous investigators have made great progress in analyzing and interpreting naturally occurring salivary gland chromosome changes, and in comparing them with similar ones induced in the laboratory. The question of the applicability of the results reported for *Drosophila* to biological material in general is one of great moment and one which can only be answered by making comparable studies on other material.

Next to *Drosophila*, the best known genus from this standpoint is *Sciara* (Mycetophilidae). This generic group is particularly favorable for comparison with *Drosophila* because it is taxonomically far removed from the latter and because its chromosomes are equally favorable for study.

As is now well known, each giant salivary gland "chromosome" consists of a pair of intimately synapsed homologues, and has its own particular pattern of cross bands or discs. Thus, microscopically visible chromosome alterations are readily detected in heterozygous individuals by examination of the disc patterns. The method has been used for study of both naturally occurring altera-

tions and artificially induced changes. For a review see "Genetics and the Origin of Species" (Dobzhansky, 1941).

In *Drosophila*, studies have established the following types of chromosome aberrations (changes): (1) inversions of one or more blocks of bands, (2) translocations of regions within the same chromosome and between chromosomes, (3) "repeats" or duplications of small regions, and (4) deletions of one or more bands.

In studies of *Sciara ocellaris* Comst., and of hybrids between this species and *S. reynoldsi* Metz, Metz (1938a) and Metz and Lawrence (1938) found evidence of considerable difference between *Sciara* and *Drosophila* with respect to chromosome changes occurring in nature.

In *Drosophila*, inversions are common among the different strains of the same species, and species hybrids usually differ from each other by numerous inversions. Minute changes in the salivary chromosomes, such as alterations in the appearance of single discs or small clusters of discs, are relatively rare but have been described in several hybrids, among them *D. melanogaster* by *D. simulans* (Kerkis, 1937, Horton, 1939).

The studies by Metz and Metz and Lawrence cited above on hybrids between *Sciara ocellaris* and *S. reynoldsi* showed no evidence of major chromosome inversions. Minute changes were readily found in different strains of *S. ocellaris* and seemed to be the main mode of differentiation between the hybrid chromosomes studied.

The present investigation represents an extension of the *Sciara* studies designed to ascertain whether or not conditions are the same in different species of this genus and whether there is general indication that the genus as a whole differs from *Drosophila* with respect to evolutionary chromosome changes.

It has been found that small differences involving only one or a small cluster of discs do seem to be characteristic of the genus *Sciara*, as distinguished from *Drosophila*, but that the findings of Metz (1938a) and Metz and

Lawrence (1938), which indicate an absence of large chromosome rearrangements, do not apply to the genus as a whole.

The present investigation has revealed a general tendency in *Sciara* for "repeats" to be associated with the X chromosome. Such a phenomenon has not been encountered in *Drosophila* and at present remains without interpretation in *Sciara*. In addition to the study of the salivary gland chromosomes, other observations, described below, were made in order to supplement those of earlier observers.

The sex ratios in the genus *Sciara* were found by Metz (1925, 1926b, 1938b) to be determined by the mother irrespective of the male and were found to vary from the common 1:1 ratio. In some species, *e.g., Sciara coprophila,* individual females produce unisexual progenies; *i.e.,* either males or females; in other species, *e.g., Sciara prolifica,* individual females regularly produce bisexual progenies. Hence, the kind of progeny produced by each of the species studied in this paper has been recorded with interest.

In this paper the term *progeny* will be used to refer to all of the offspring from any individual female. Species in which the individual females produce offspring of only one sex, either male or female, will be said to produce unisexual progenies. Species in which the individual females regularly produce both males and females will be said to produce bisexual progenies. It is important to note that females of species which produce unisexual progenies do occasionally produce "exceptional" individuals of the opposite sex. However, no attempt has been made to check the frequency of occurrence of these "exceptional" individuals. Further it should be noted that sex ratios were not recorded for the species discussed in this paper which produce bisexual progenies.

In addition to the group of "ordinary" specific chromosomes, earlier studies in *Sciara* revealed different numbers of "limited" chromosomes, depending on the

species (see Metz, 1938b, for a review of the conditions in *Sciara*). "Limited" chromosomes are usually larger than the others and appear to have a greater diameter. Although these chromosomes are apparently genetically inert or nearly so, they reproduce and go through the mitotic process with the other chromosomes. The "limited" chromosomes number from one to three in those species which possess them and are restricted to the germ line. They are eliminated from the soma at either the fifth or the sixth cleavage division of the egg (Dubois, 1933).

Since the significance of the "limited" chromosomes is still obscure, attention has been directed in this investigation toward determining their presence or absence, their numbers and their morphological character for each of the eight species studied.

Metz and Moses (1923) have shown in a survey of the somatic chromosome groups of a number of species of *Drosophila* that the different species have different chromosome numbers. Nearly all the variations, however, could be explained by assuming appropriate rearrangements of the chromatin of the basic number of four chromosome pairs, *e.g.,* fusion of rods to form V's, conversion of V's to rods, etc. It seems probable that these rearrangements have been significant in the evolutionary process (see Sturtevant and Novitsky, 1942). A similar study of the somatic chromosome groups of the eight species of *Sciara* reported here has been made to determine whether or not similar forces affecting chromosome rearrangements are operating within this genus.

The author is indebted to Dr. Metz for suggesting the problems investigated, for his help in carrying them out and for his advice and help in the preparation of this manuscript.

MATERIALS AND METHODS

1. ESTABLISHMENT AND IDENTIFICATION OF CULTURES

The stocks of the several species of *Sciara* studied were all established in the same manner. Collecting trips to a

number of greenhouses were made wherein single gravid
females were trapped on the glass by covering them with
small vials partially filled with agar.   The vials with
the single females were returned to the laboratory and
kept at room temperature to await the laying and hatch-
ing of eggs.   Subsequent generations were reared ac-
cording to the procedure outlined by Smith-Stocking
(1936).

About a thousand females were captured, representing
about thirty different species of which only eight gave
rise to laboratory stocks.   The different species were
designated with Roman numerals and collections of each,
composed of pinned specimens, alcoholic specimens, wing
mounts and hypopygial mounts, were made.   The author
wishes to thank Dr. Frank R. Shaw for examining some
of the material and identifying species V as *Sciara nacta*
Johannsen, and Dr. Alan Stone for his advice and kind-
ness in examining specimens of each species and identi-
fying species IV and VI as taxonomically the same, being
Sciara fenestralis Zetterstedt; species XV–6 as *Sciara
prolifica* Felt, Johannsen's variety b; and species XXIV
as *Sciara agraria* Felt.   The other species, namely VII,
XXIII and XXV, Dr. Stone reports as undescribed;
hence, they will be referred to by Roman numerals
throughout this paper.

Although IV and VI are morphologically similar and
have been called the same species by Dr. Stone, the author
believes them to be distinct species and will treat them as
such for the following reasons:

a. Examinations of wing mounts of the two forms show the petiole of the
    cubitus to be about .8 that of the basal section of the media in IV and
    only .5 in VI.
b. Species IV females are ''bisexual producers''; *i.e.*, individual females of
    this form *regularly* produce both males and females, with males in excess.
    In contrast, species VI females are *regularly* '' *unisexual producers*''; *i.e.*,
    individual females of this form regularly produce one sex, either males
    or females.   Exceptional individuals occur in both types of progenies.
c. Reciprocal crosses failed to produce hybrids between these forms.
d. Banding patterns of the salivary gland chromosomes do not match in the
    case of the X chromosomes, nor do they match in the cases of the other
    similar length chromosomes.

c. Other cases such as this are on record; *e.g.*, Dobzhansky's *Drosophila pseudoobscura* a and b (Tan, 1935), or Metz's *Sciara ocellaris-reynoldsi* case (Metz and Lawrence, 1938).

Hence, I shall refer to IV as *Sciara fenestralis* form I and to VI as *S. fenestralis* form II.

2. GONIAL METAPHASE FIGURES

Gonial metaphase figures were obtained by dissecting out the gonads of larvae two to five days after hatching. The dissection was made in Ringer's solution. The excess Ringer's was drawn off and a small drop, 3 mm in diameter, of acetocarmine added. Immediately the gland was smeared by dropping a cover slip on it. The edges of the cover slip were ringed with vaseline and the preparation allowed to stand for twelve hours in a moist container. The preparation was made permanent by the following procedure: the vaseline was removed and the slide placed cover slip down supported by two glass rods in a petri dish containing a mixture of equal parts of glacial acetic acid, 95 per cent. alcohol and clove oil; when the cover slip had floated off, either the slip or the slide, to whichever the gland adhered, was washed in two changes of 95 per cent. alcohol after which it was mounted in diaphane.

3. SOMATIC METAPHASE GROUPS FROM CEPHALIC GANGLIA AND SALIVARY GLAND PREPARATIONS

Cephalic ganglia and salivary glands were dissected out in body fluid and immediately transferred to a small drop, 3 mm in diameter, of 45 per cent. acetic acid on a clean glass slide. The glands and ganglia were smeared by dropping a cover slip on them. The preparation was placed in 95 per cent. alcohol vapor for three hours; then the cover slip was soaked off in 95 per cent. alcohol. The slip or slide bearing the material was returned to 45 per cent. acetic acid for one minute, thence into acetocarmine for five minutes. The stained preparation was rinsed in 95 per cent. alcohol, passed quickly through a 45 per cent. acetic acid bath to remove excess stain, dehydrated 5 minutes in 95 per cent. alcohol, and mounted in diaphane.

The somatic chromosome groups show that all species studied have the same diploid chromosome number, namely, eight.   The shapes and sizes of the chromosomes, however, differ in different species.

The gonial chromosome groups show, in some cases, chromosomes which have no homologues in the soma. These chromosomes have been referred to in the introduction as "limited" chromosomes. Like the "ordinary" chromosomes, these, too, differ in size and shape. Particular attention should be called to the fact that so far as observed those species having rod-shaped "limited" chromosomes have two of them.   This point will be emphasized in the discussion.

For each of the eight species studied, both ends of each of the salivary gland chromosomes have been mapped in addition to regions of special interest, such as asynaptic regions, repeated regions, etc.   In discussing the salivary gland chromosomes of each species studied, the longest autosomal chromosome in each complex will be referred to as the A chromosome, the next longest as the B and the shortest as the C.   This grouping does not imply that all A chromosomes, for instance, are homologous; but merely that each represents a similar proportionate length with respect to the other chromosomes in each of the several species complexes.

The findings with respect to the features mentioned above will be presented for each species separately, together with information concerning the source of material, distribution of the species when obtained in more than one place and any special remarks.

<div align="center">Observations</div>

<div align="center">*Sciara agraria* Felt</div>

<div align="center">1. SOURCE AND GENERAL CHARACTERISTICS</div>

The laboratory stock from which the following data were obtained was established by making brother-sister matings from the offspring of one of several females collected from a flower pot in a residence in Telford, Pa.

This species grows well in the laboratory. It has been secured in two other localities within a forty-mile radius of Telford. Individual mated females of this species produce bisexual progenies.

2. SOMATIC AND GONIAL METAPHASE CHROMOSOMES

The somatic chromosome complex (Fig. 6b) shows two pairs of V-shaped chromosomes and two pairs of rod-shaped chromosomes. The gonial metaphase chromosome group (Fig. 6a) shows three pairs of V's and two pairs of rods. One pair of V's is decidedly larger than the other two pairs. The large V-shaped chromosomes with no counterparts in the soma are the "limited" chromosomes. The "limited" chromosomes are eliminated from the soma at an early cleavage division, as mentioned above.

3. SALIVARY GLAND CHROMOSOMES

The salivary gland chromosomes in this species spread easily and stain well; hence, they offer no technical difficulties. Figs. 9a and 9b show the two ends of the C chromosome. The two ends of the A chromosome are shown in Figs. 11a and 11b. There were no irregularities found in these two chromosomes.

Small differences between homologues. Figs. 12a and 12b represent the two ends of the B chromosome. The arrow in Fig. 12a indicates a small difference in banding pattern. Either one band in one homologue is missing or an extra one is present in the other. In this case, the extra band in the one homologue was sufficient to cause a small asynaptic gap between the two homologues.

"Repeats." Fig. 10a shows one end of the X chromosome in which there has been a duplication of a short region of the chromosome. These two homologous portions of the chromosome have synapsed to form a short, tight loop. Fig. 10b shows the other end of the X chromosome.

Rearrangements. In the material examined representing this species, no large rearrangements were found, but

not enough specimens were secured to show that such re-
arrangements do not occur in the species.

Sciara species XXV

1. SOURCE AND GENERAL CHARACTERISTICS

Several females of this species were collected in a
greenhouse in Norwood, Pa. The species thrives in the
laboratory and mated females produce bisexual progenies
in which neither sex occurs in great excess of the other.
This species was found only once and is undescribed.

2. SOMATIC AND GONIAL METAPHASE CHROMOSOMES

The somatic metaphase chromosome group (Fig. 5b),
like the gonial metaphase chromosome group (Fig. 5a),
shows one pair of V-shaped chromosomes and three pairs
of rod-shaped chromosomes. This species, according to
this material, possesses no "limited" chromosomes, a
characteristic wherein it resembles *Sciara ocellaris* and
S. reynoldsi. Metz and his students have studied the
latter two species extensively and have not yet found a
race which possesses "limited" chromosomes. Hence, it
is likely that the "limited" chromosomes have been lost
from these species.

3. SALIVARY GLAND CHROMOSOMES

The ends of the salivary gland chromosomes in this
species are sufficiently different from each other so that
no difficulty is experienced in differentiating between
them. The two ends of the A chromosome are seen in
Figs. 14a and 14b. Figs. 15a and 15b represent the two
ends of the C chromosome. Figs. 16a and 16b show the
two ends of the B chromosome.

*Rearrangements and small differences between homo-
logues.* In this particular stock no small differences and
no large chromosome rearrangements were observed.
But as has been mentioned above for a similar case, this
does not necessarily mean that these phenomena do not
occur in this species.

"Repeats."   One end of the X chromosome (Fig. 13a) shows two similar regions of at least three bands which are not tightly synapsed in this figure but are spread apart, remaining connected by several heterochromatic strands.   In most of the cells examined, this repeated region was more tightly synapsed, allowing but a very limited view of the duplicated region.   The banding pattern of the other end of the X chromosome is shown in Fig. 13b.

Sciara prolifica Felt Johannsen's var. b

1. SOURCE AND GENERAL CHARACTERISTICS

The laboratory stock of *S. prolifica* from which these observations were recorded was started from brother-sister matings of the offspring of a single female which was collected in a greenhouse in Johnson City, Tenn. Several females were collected at the same time in the same greenhouse.   However, material from only one of them was used in building up a laboratory stock.   Mated females of this species produce bisexual progenies.   This species has been found in nearly every greenhouse examined from New York to South Carolina where horse manure is used.   In addition to the greenhouse collections, this species was obtained in great numbers around a pile of chicken manure, in an open meadow in Ridley Park, Pa.

In addition to preparations made from the stock which was selected as a type, a few preparations were made from offspring of four different collections.   The Tennessee stock was maintained because it contained both a "repeat" and a chromosome rearrangement, whereas the other stocks had only the "repeat."   To investigate the potentialities of these various stocks by cross breeding was not thought profitable, since Mr. Carson was making such a comprehensive study for *Sciara impatiens.*

2. SOMATIC AND GONIAL METAPHASE CHROMOSOMES

The somatic metaphase chromosome group (Fig. 8b) is composed of two pairs of V-shaped chromosomes and two

pairs of rod-shaped chromosomes. The gonial meta-
phase group (Fig. 8a) shows one large V-shaped chromo-
some in addition to those chromosomes which are homol-
ogous to the chromosomes in the somatic metaphase. This
large V-shaped chromosome is the "limited" chromo-
some.

3. SALIVARY GLAND CHROMOSOMES

The salivary gland chromosomes of this species are
quite different in appearance from those of the other
species examined. They are short, thick and grossly
resemble short pieces of rope. They separate from each
other readily when smeared, and stain easily. However,
it is difficult to obtain the larvae in the stage in which
the stained bands of the salivary chromosomes are
sharply delimited from each other. Figs. 18a and 18b
show the two ends of the A chromosome. Figs. 20a and
20b show the two ends of the B chromosome. The distal
tip of the B chromosome (Fig. 20b) is doubled back on
itself. This was a characteristic of this end of the B
chromosome which manifested itself in different ways.
In some preparations this tip was pulled away from the
rest of the chromosome, maintaining only a thin hetero-
chromatic strand connection.

Small differences between homologues. No small dif-
ferences were found in the Tennessee stock, which was
studied intensively. Only a limited study was made of
the ends in the other stocks; these did not show any small
differences. Thus, evidence is not conclusive as to the
occurrence of minute changes in this species.

"Repeats." Fig. 19a shows one end of the X chromo-
some. Fig. 19b shows the mid-region of the X chromo-
some. The small check marks opposite the bands in
Figs. 19a and 19b indicate that these are the same bands.
Fig. 19c represents the other end of the X chromosome.
The two ends (Figs. 19a, 19c) were drawn from a dif-
ferent cell than was the mid-region of the X chromosome
(Fig. 19b). The mid-region of this chromosome shows a
double looped configuration. This was caused by the

synapsis of the three similarly banded regions, the pattern of which was not clear in any slide.   This is an example of a double "repeat."

Rearrangements.   Fig. 17 shows the C chromosome in which there has been an inversion involving about three fourths of the length of this chromosome.   This figure, as well as all others of this inversion, indicates this to be a terminal inversion; that is, one involving the entire distal tip of the chromosome.   Slides of three of the four other stocks did not show this inversion.   The slides of the fourth stock showed the inversion, but the banding pattern was not good enough to admit of analysis.

Sciara species XXIII

1. SOURCE AND GENERAL CHARACTERISTICS

This species was taken independently by two different collectors in greenhouses in Wilmington, N. C.; Columbia, S. C.; and Charleston, S. C.   Offspring from one of the females collected in Wilmington provided the sibs used in establishing the laboratory stock from which the following data have been secured.   A few slides were made from the F_1 larvae of the females collected at the other two cities also.   This species gives rise to bisexual progenies.

2. SOMATIC AND GONIAL METAPHASE CHROMOSOMES

The somatic chromosome group (Fig. 3b) shows a variation in the shape of the chromosomes.   There are no V-shaped chromosomes present, but four pairs of rods.   The gonial group (Fig. 3a), like the somatic group, has all rod-shaped chromosomes.   In addition to those chromosomes which are homologous to those in the soma, there are two large, unpaired, rod-shaped chromosomes.   These are the "limited" chromosomes.

3. SALIVARY GLAND CHROMOSOMES

The salivary gland chromosomes of this species seemed to be exceptionally long.   Many slides showed cells in which the four chromosomes were joined together, the joined ends forming a hub from which the chromosomes

radiated.   Examination of those cells in which the chromosomes were joined and those in which the chromosomes were not joined showed that (a) the same chromosome ends were always united in the joined state and (b) in the unjoined state the ends homologous to the uniting ends were often ragged with heterochromatic material protruding from them.   Fig. 23a shows such a condition in end 1 of the C chromosome.   This behavior of the salivary chromosomes is similar to that found in *Sciara reynoldsi* and is suggestive of the chromocenter condition which is found in *Drosophila*.   Fig. 23b shows the other end of the C chromosome.   Fig. 21a shows the banding pattern of end 1 of the A chromosome.   Although this chromosome end is broken in this figure, all the bands are present.   End 2 of the A chromosome is seen in Fig 21b.

Small differences between homologues.   One small difference was found is several cells from one individual in this species.   This is shown in Fig. 22a, which is end 1 of chromosome B.   The arrow in this figure indicates a thin band opposed to a thick band.   Fig. 22b represents end 2 of the B chromosome.

"Repeats."   The X chromosome in this species has a single duplicated region.   When these two homologous regions synapse, a short looped figure is produced (Fig. 24b).   This is a typical "repeat" figure in which the homologous regions have become linearly separated.   As in most of these "repeats," the banding pattern is confused and determining how many bands are involved is difficult.   Fig. 24a shows end 1 of the X chromosome.   This figure, like 23a, shows the sticky attenuated condition of the end which is in many cases joined to the ends of the other chromosomes.   Fig. 24c represents end 2 of the X chromosome.

Rearrangements.   No large rearrangements were found in any of the three stocks of this species examined.   Again, however, there is insufficient evidence to say that gross rearrangements do not occur in this species.

<div align="center">(To be concluded)</div>

Figures on Plate I are camera lucida drawings at a magnification of 2,100 diameters. Figures on Plates II, III, IV and V are camera lucida drawings, all at the same magnification as indicated by the scale on each plate. Figures on Plate VI are photomicrographs. Fig. 45 was photographed at the magnification indicated by a scale just under it; all other figures are at the magnification indicated by a scale above Fig. 41. All figures on Plate VII are outline drawings, drawn with the aid of a camera lucida. The magnification scale beneath each figure represents .1 mm.

EXPLANATION OF FIGURES, PLATE I

1a, 1b, *Species VII.* Gonial metaphase group (4 pairs of rods—1 pair of V's), somatic metaphase group (3 pairs of rods—1 pair of V's). "Limited" chromosomes in 1a are indistinguishable.

2a, 2b, *Sciara nacta.* Gonial metaphase group (5 pairs of rods), somatic metaphase group (4 pairs of rods). Difficult to distinguish "limited" chromosomes, probably the two largest rods in 2a.

3a, 3b, *Species XXIII.* Gonial metaphase group (5 pairs of rods), somatic metaphase group (4 pairs of rods). Difficult to distinguish "limited" chromosomes.

4a, 4b, *Sciara fenestralis,* form I. Gonial metaphase group, (2 pairs of rods—3 pairs of V's), somatic metaphase group (2 pairs of rods—2 pairs of V's). The large V-shaped chromosomes at the bottom of figure 4a are the "limited" chromosomes.

5a, 5b, *Species XXV.* Gonial and somatic metaphase groups (3 pairs of rods—1 pair of V's). No "limited" chromosomes.

6a, 6b, *Sciara agraria.* Gonial metaphase group (2 pairs of rods—3 pairs of V's), somatic metaphase group (2 pairs of rods—2 pairs of V's). The two large chromosomes in the lower left hand corner of figure 6a are the "limited" chromosomes.

7a, 7b, *Sciara fenestralis,* form II. Gonial metaphase group (2 pairs of rods—2 pairs of V's—1 single large V), somatic metaphase group (2 pairs of rods—2 pairs of V's). Large single V in 7a is the "limited" chromosome.

8a, 8b, *Sciara prolifica,* Johannsen's var. b. Gonial metaphase group (2 pairs of rods—2 pairs of V's—1 large single V), somatic metaphase group (2 pairs of rods—2 pairs of V's). Large single V in 8a is the "limited" chromosome.

EXPLANATION OF FIGURES, PLATE II

9-12 *Sciara agraria.* Salivary gland chromosomes.

9a   End 1 of "C" chromosome.

9b   End 2 of "C" chromosome.

10a   End 1 of "X" chromosome with "repeat" region shown about one third the length of the chromosome from end 1.

10b   End 2 of "X" chromosome.

11a   End 1 of "A" chromosome.

11b   End 2 of "A" chromosome.

12a   End 1 of ''B'' chromosome.   Arrow in this figure indicates a small difference in banding pattern in which one band in one homologue is missing.

12b   End 2 of ''B'' chromosome.

13–16   *Sciara species XXV.*   Salivary gland chromosomes.

13a   End 1 and mid-region of ''X'' chromosome including ''repeat'' regions which have been pulled apart leaving a thin strand between them.

13b   End 2 of ''X'' chromosome.

14a   End 1 of ''A'' chromosome.

14b   End 2 of ''A'' chromosome.

15a   End 1 of ''C'' chromosome.

15b   End 2 of ''C'' chromosome.

16a   End 1 of ''B'' chromosome.

16b   End 2 of ''B'' chromosome.

EXPLANATION OF FIGURES, PLATE III

17–20   *Sciara prolifica* (Felt), Johannsen's var. b.   Salivary gland chromosomes.

17   Terminal inversion of ''C'' chromosome involving two thirds of the length of the chromosome.

18a   End 1 of ''A'' chromosome.

18b   End 2 of ''A'' chromosome.

19a   End 1 of ''X'' chromosome.

19b   Extended regions of ''X'' chromosome showing ''double repeat'' in which the three homologous regions are synapsed.   The check mark opposite the dark band of 19a and that opposite the dark band in figure 19b indicate that the two bands are the same.

19c   End 2 of ''X'' chromosome.

20a   End 1 of ''B'' chromosome.

20b   End 2 of ''B'' chromosome.

21–24   *Sciara species XXIII.*   Salivary gland chromosomes.

21a   End 1 of ''A'' chromosome.

21b   End 2 of ''A'' chromosome.

22a   End 1 of ''B'' chromosome.   Arrow in this figure shows a thick band in one homologue apposed to a thin band in the other.

22b   End 2 of ''B'' chromosome.

23a   End 1 of ''C'' chromosome.   ''Sticky'' condition of the end indicated by the material extending from the vesicle.   The same sort of condition is shown in 24a.

23b   End 2 of ''C'' chromosome.

24a   End 1 of ''X'' chromosome.

24b   Mid-region of ''X'' chromosome showing synapsis of two homologous regions (''repeat'').

24c   End 2 of ''X'' chromosome.

PLATE I

1a   1b   5a   5b

2a   2b   6a   6b

3a   3b   7a   7b

4a   4b   8a   8b
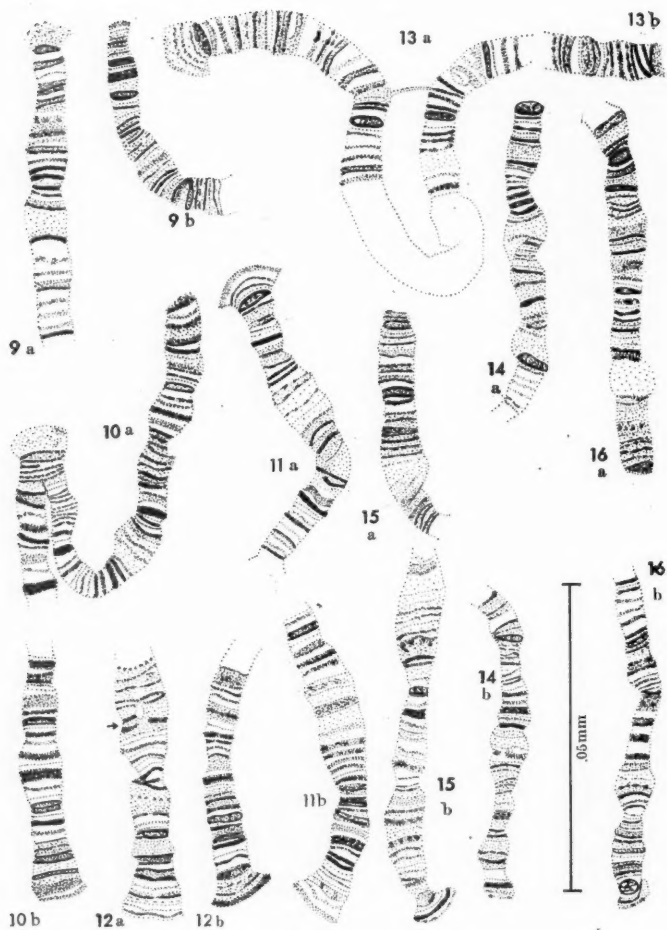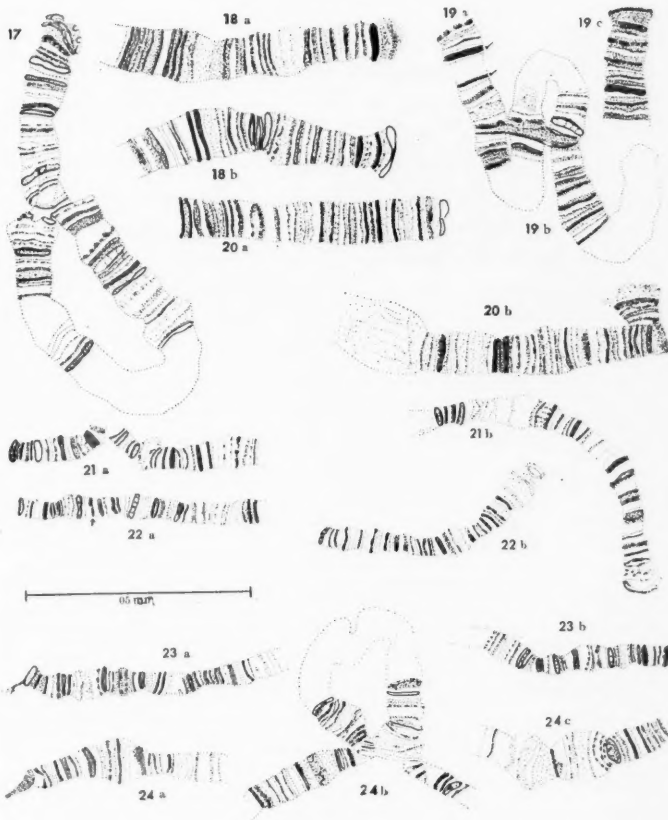
PLATE II

PLATE III

THE BISEXUALITY OF UNIPARENTAL HYMENOPTERA, A FUNCTION OF THE ENVIRONMENT[1]

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REPRODUCTION in the Hymenoptera is characterized by the production of uniparental apomictic[2] individuals. The normal male, always uniparental, is haploid. The female, either uniparental or biparental, is diploid.

In a uniparental species, the progeny of unmated females are usually females; in a biparental species, usually males. There is, however, in many if not all hymenopterous species, a capacity to produce both sexes uniparentally (amphitoky). This uniparental bisexuality, as recorded for a number of hymenopterous species, appears to be an effect of environmental factors.

The purpose of this paper is to present evidence supporting the thesis that the sexuality of a uniparental population is an expression of the type of germinal tissue in the preceding generation, the type being determined by environmental conditions. The observations forming the basis of this study were made during the mass propagation of beneficial insects at the University of California Citrus Experiment Station, Riverside, California.

THE PREVALENCE OF UNIPARENTAL REPRODUCTION IN THE HYMENOPTERA

The species of the order Hymenoptera form two more or less distinct groups: a biparental group, in which, under usual conditions, all males and only a few females are uniparental; and a uniparental group, in which, under usual conditions, all females and all males are uniparental.

The sawflies (Tenthredinidae) commonly reproduce

uniparentally (Imms, 1934). At least 30 genera of the parasitic Hymenoptera contain one or more species that reproduce uniparentally (Clausen, 1940). In a majority of the 16 species of the phytophagous genus *Harmolita*, studied by Phillips (1920), reproduction is uniparental.

According to Clausen (1940), it is rather surprising that the uniparental reproduction of females has not yet been found to occur in the Serphoidea.

In some species of Hymenoptera, uniparental and biparental reproduction are racial characters. This is most apparent when such races are segregated geographically, as with those of *Hemiteles arcator* and *Eupelmella vesicularis*, which are uniparental in North America and biparental in Europe (Muesebeck and Dohanian, 1927); also with those of *Leucospis gigas*, which are uniparental in Europe and biparental in North Africa (Berland, 1934); of *Trichogramma embryophagum*, which are biparental in North America and uniparental in Europe; and of *Thripoctenus brui*, which are uniparental in Europe and biparental in Japan (Clausen, 1940).

This differentiation in reproduction appears to be dependent on the production of two kinds of eggs: type I, yielding only uniparental females, and type II, yielding biparental females as well as uniparental males. Any species may be capable of producing both type-I and type-II eggs, but most of the eggs deposited by any one species are of one type. This is indicated by the fact that in uniparental species males are relatively uncommon and biparental females extremely rare, while in biparental species males and biparental females usually are common and uniparental females uncommon. In any species the type-I egg and the fertilized type-II egg may be genetically equal.

The Prevalence of Uniparental Bisexuality

There are relatively few recorded observations on the bisexuality of uniparental broods[3] of biparental species

[3] The term *brood*, as used in this paper, comprises *all* the mature offspring of a single female.

or races.   This may have been in part because observers
have viewed with suspicion the occurrence of uniparental
females in biparental species and have regarded such an
occurrence as evidence of faulty technique in the handling
of material.

Uniparental females have been recorded as occurring in
the biparental species *Apis mellifica* (Mackensen, 1943),
Pteromalus puparum (Adler, 1894), *Lasius niger* (Reich-
enbach, 1902), *Lysiphlebus testaceipes* (Hunter, 1910;
Webster and Phillips, 1912), *Campsomeris trifasciatus*
(Box, 1925), *Ephialtes extensor* (Rosenburg, 1934),
Microbracon hebetor (Speicher and Speicher, 1938), and
in the biparental race of *Diprion polytomum* (Balch,
Reeks and Smith, 1941).

Many species hitherto recorded as biparental, because
the male sex comprises a large part of the population and
mating readily occurs, actually may be uniparental in
reproduction.   If the females of a bisexual species such
as the ichneumonid *Opheltes glaucopterus* produce only
unisexual broods (Bischoff, 1927), uniparental reproduc-
tion may be suspected.   Species are probably biparental
if, when reproducing under optimum conditions, the un-
mated females produce only males.

Apparently, the bisexuality of uniparental populations
of Hymenoptera is most marked in the alternate genera-
tions of the gall wasps (Cynipidae).   The males in the
uniparental spring generation are numerous, and mating
readily occurs.   While mating may or may not be neces-
sary for the genesis of overwintering-generation females,
it appears to be a prerequisite of oviposition by the par-
ental spring generation.   In certain cynipids and in other
species of uniparental Hymenoptera, however, such as
Habrolepis rouxi Compere and *Encarsia formosa* Gahan,
the female appears to have lost the mating instinct.

The bisexuality of uniparental populations varies
within species as well as between species.   Speicher and
Speicher (1938) noted that uniparental females of *Micro-
bracon hebetor* were obtained almost entirely from bipar-

ental females resulting from crossing certain strains. The uniparental females regularly constituted about 1 per cent of the total progeny of unmated biparental females. Smith (1941) reported that the uniparental race of *Diprion polytomum* in Canada appeared to consist of strains differing in the frequency of male production.

Apparently, the bisexuality (amphitoky) of uniparental hymenopterous populations verges toward total femaleness (thelyotoky), as in the sawflies, or toward total maleness (arrhenotoky), as in the serphoids.

UNISEXUAL AND BISEXUAL BROODS IN RELATION TO HABITAT AND SEASONAL DEVELOPMENT

Whenever unisexual and bisexual broods have been noted as occurring in a uniparental species, there has appeared to be a distinct correlation between the sexuality of the broods and the type of habitat or the season in which development occurred, the conditions under which one generation developed apparently predetermining the sexuality of the following generation. Such a correlation has not been noted in the case of biparental species, probably because of insufficient data.

Uniparental Species in which Developmental Conditions May Cause the Production of Type-II Eggs

Since the type-II egg is not predominant and usually is rare in most uniparental species developing under optimum conditions, it is in such species that the effect of environmental changes on the production of type-II eggs is most readily discernible.

Male production correlated with temperature. Although Speyer (1926–27) stated that, in the uniparental *Encarsia formosa*, parasitic on the greenhouse whitefly, low temperatures preceded the occurrence of male adults, his data show that the parents of the males developed during a period when temperatures were high, 7 males appearing among 100 specimens that emerged during September.

The uniparental chalcid *Harmolita grandis* oviposits in stems of winter wheat and, like many of the gall-forming cynipids, exhibits generations alternating in habitat, form, and sexuality, a unisexual overwintering generation consisting of perfectly winged females developing from eggs deposited during May, and a bisexual generation in which the females are wingless or imperfectly winged developing from eggs deposited during March (Phillips and Emery, 1919; Phillips, 1920).

Several species of uniparental mymarids of the genera *Anagrus* and *Paranagrus* were reared continuously from January to the middle of September, in Hawaii, where a generation occurred every three weeks. Males appeared only in September, the progeny of females that developed during August, the warmest month of the year in that area (Perkins, 1905).

In the uniparental race of the spruce sawfly, *Diprion polytomum*, males are rarely found in the field, and constitute only about 0.09 to 0.38 per cent of the population. Higher percentages are observed in the warmer regions. When this race is propagated at temperatures exceeding 70° F, the sex ratio may be 1 male to 37 females (Smith, 1941).

The chalcid *Ditropinotus aureoviridis* exhibits a unisexual overwintering generation and a bisexual summer generation (Phillips and Poos, 1921).

The writer has found that, with the uniparental chalcid *Habrolepis rouxi*, the production of unisexual or bisexual broods may depend on the environmental conditions to which the parent females are subjected during their early larval stages. Females that develop at temperatures of 80° F, or less, in healthy *mature* red scale, *Aonidiella aurantii* (Mask.), infesting freshly picked grapefruit are thelyotokous, producing only unisexual (female) broods. Females subjected to a constant temperature of 90° F during early larval development in *immature* hosts are usually either amphitokous or arrhenotokous, producing bisexual broods or unisexual (male) broods.

Male production correlated with nutrition. The uni-parental braconid *Microctonus brevicollis,* a parasite of the beetle *Haltica ampelophaga,* in Algeria, exhibits generations alternating in habitat and sexuality, a unisexual generation that develops from eggs deposited in the host larvae alternating with a bisexual overwintering generation that develops from eggs deposited in the adult of the host species (Künckel d'Herculais and Langlois, 1891).

Van Rossum (Bischoff, 1927) observed that the various species of sawflies feeding on alder are to a great extent unisexual, while very closely related species feeding on birch are bisexual.

The chalcid *Prospaltella perniciosi* Tower is bisexual when reproducing on San Jose scale growing on peach trees and unisexual when reproducing on San Jose scale growing on the cow melon (*Citrullus vulgaris*) in the laboratory (Flanders, 1944).

The bisexuality of the uniparental gall-forming eurytomid *Trichilogaster acaciae-longifoliae* varies with different species of host plants, *Acacia longifolia* var. *floribunda* yielding males and females in about equal numbers, while the number of males yielded by *A. longifolia* is about 1 per cent of the population. It is significant that in ovipositing on *A. longifolia,* the female selects only the developing flower buds, whereas on *floribunda* it oviposits in the tips of young branches as well as at the points where flower buds develop (Noble, 1940).

Biparental Species in which Developmental Conditions May Cause the Production of Type-I Eggs

Species in this group are entirely or largely biparental in reproduction; that is, most of the females are arrhenotokous, and the few that produce type-I eggs are amphitokous. In this group it should be noted that the sex ratio may be modified by post-oogenic factors.[4]

[4] In species that reproduce biparentally, the sex ratio of any generation may be changed by the differential mortality of eggs and larvae. When fertilization is necessary for the production of females, then the sex of the deposited egg is determined by the rate of oviposition and the degree of preferential oviposition (Flanders, 1939).

In 1876, Adler (1894) observed uniparental bisexual production in the biparental chalcid *Pteromalus puparum.* The broods of two unmated females consisted of 75 males and 5 females, and of 45 males and 4 females, respectively.

In a series of experiments by Kelly and Urbahns, in 1908, (Webster and Phillips, 1912), 3 unmated females of the biparental braconid *Lysiphlebus testaceipes* produced broods as follows: 70 males and 3 females, 101 males and 6 females, and 67 males and 1 female. An unmated female of one of these broods reproduced so that a second generation of uniparental females was obtained.

Hunter (1910) records bisexual broods from 7 unmated females of *Lysiphlebus testaceipes.* Hase (1922), from an unmated female of *Microbracon hebetor,* reared 16 males and 14 females. Moursi (1943) obtained 3 uniparental females of *Mormoniella vitripennis* in a brood consisting of 162 individuals. The time of their emergence indicated that they were derived from the first eggs deposited by the mother. These were the only females among 15,925 individuals reared during the experimental work.

The wheat stem sawfly, *Cephus cinctus,* has been assumed to be biparental in most of the infested districts of Canada, since in these areas the sexes occur in about equal numbers. Significantly, however, in certain districts of Alberta, where the sawfly recently has become established, only females are produced (Farstad, 1938).

Mackensen (1943) states that in the domestic strains of the honeybee in the United States, uniparental females occur more commonly than hitherto believed. Of 50 virgin queens producing enough offspring to make a good test, 21 produced bisexual broods. The number of female offspring produced by any one virgin queen was estimated not to exceed 1 per cent.

In certain species of solitary bees of the genus *Halictus,* Fabre (1879) observed uniparental bisexual generations that developed during the summer, alternating with biparental unisexual generations that developed during the

spring.   In this case the females of the unisexual genera-
tions produced type-I eggs *in addition to* type-II eggs.
This is the reverse of the condition noted in the case of
Harmolita.

The Production of Type-I and Type-II Eggs in the Cynipids

The cynipids present many interesting examples of a
definite correlation between alternating habitats and sea-
sons and alternating bisexual and "agamic" (unisexual)
generations. In certain species the females of the
"agamic" (supposedly biparental) generation are of two
types (Patterson, 1928b) : the ovaries of one type of
"agamic" female are thelyotokous, and those of the
other type arrhenotokous.   The ovaries of the females of
the bisexual generation are largely if not entirely of one
type, however, as indicated by the fact that their progeny
are usually female.

The occasional unfertilized type-II egg deposited by the
bisexual generation may not hatch because of the unsuit-
ability of the plant tissues in which it is deposited.   This
is not a unique phenomenon, for the unfertilized type-II
eggs deposited by *mated* females of several species of
the chalcid genus *Coccophagus* never hatch (Flanders,
1937).   The few males of the "agamic" generation
reaching maturity may never mate, since their sibs lack
the mating instinct (Patterson, 1928a).

The alternation of a generation in which females are
of one reproductive type with a generation in which the
females are of two reproductive types appears to be an
effect of nutrition—an effect possibly enhanced by differ-
ences in temperature during development.   The chemical
constitution of the concentrated nutriment in which the
larvae of each alternating generation are immersed may
differ because of differences in the reaction of different
parts of the host plant to the secretions of the larvae.[5]

[5] The form of the gall produced by the cynipid depends on the species of
insect rather than on the species of plant (Kinsey, 1929).   The host plant
produces the gall under stimulation of a glandular fluid secreted by the
cynipid larva (Triggerson, 1914).

Adler (1894) suggested that any differences in cynipid larvae result only from differences in the duration of their development. Duration of development, however, may be an effect of nutrition, as has been observed in the honeybee.   It is interesting to note that male production by uniparental females of *Cladocera* (Crustacea) is promoted by environmental factors that lower the rate of metabolism (Banta, 1937).

If, in the bisexual generation of cynipids, fertilization is not necessary for reproduction, then the cynipids follow the apparent rule, that the production of the type-II egg is correlated with high temperature during development.   In the bisexual generation—that is, the generation in which males are numerous and females are of one type —the females are exposed to comparatively low temperatures during early larval development and theoretically should be thelyotokous.   The "agamic" generation, consisting of females of two types (thelyotokous and arrhenotokous), is exposed to comparatively high temperatures during early larval development.

Since it is probable that it is the influence of the environment on the immature stages of the "agamic" generation which determines the proportion of type-I and type-II eggs produced by that generation, it follows that, if the broods produced by the females of the "agamic" generation are either all male or all female, then the parent of each brood developed under one of two sets of conditions, as regards food and, possibly, temperature.   If, as in the case of *Neuroterus niger,* a cynipid female tends to deposit all its eggs within a very limited area, as, for example, in one oak leaf (Patterson, 1928b), all the "grandchildren" of a bisexual-generation female may be entirely female or entirely male (Doncaster, 1917), since their parents were reared together under uniform conditions.

The females of the alternate generations of cynipid gall wasps are so different morphologically that they have been described as distinct species. This difference is

ascribed to nutrition (Salt, 1937). The fact that only a portion of the females of the "agamic" generation are thelyotokous indicates that ovarian dimorphism in this generation may result from differences in exposure to either nutritional or atmospheric conditions during development.

In the case of the uniparental cynipid *Rhodites rosae*, in which there is no alternation of generations, males and females are produced in a ratio of 1 to 130. A few galls yield only males; others yield both sexes (Callan, 1940).

It is interesting to note that the eggs produced by cynipid inquilines may be only of type II, although the females may have developed in host galls formed by host larvae destined by environmental factors to produce eggs of type I (McCracken and Egbert, 1922).

A Mechanism Producing Egg Types I and II, Subject to Environmental Control

In uniparental species of Hymenoptera, the mechanisms for retaining the diploid number of chromosomes vary widely (Speicher, 1937). In the uniparental species *Habrolepis rouxi*, it has been observed by the writer that, at normal temperatures, bisexual broods usually are produced by only a few females, and that males form only a very small part of broods developing under optimum conditions. At temperatures of about 80° F, or less, a female that happens to have the capacity for producing type-II eggs always begins to deposit such eggs within about a week after emergence from the host. Since the egg-production period of a female is considerably longer than the developmental period of its offspring, and the sexuality of the brood is apparent soon after the offspring begin to emerge as adults, it is possible to segregate those females that lack the capacity for male production *before* they deposit all their eggs. This would be an improbable situation if uniparental females were derived from type-II eggs as a result of some modification of the meiotic process.

Schrader (1920) suggested that uniparental reproduction in the cynipid *Rhodites rosae* might be an effect of the multiplication of chromosomes in the oogonia, so that after reduction the nucleus of the egg is diploid. The work of Speicher and Speicher (1938) on the biparental *Microbracon hebetor* indicates that type-I eggs in the higher Hymenoptera may be formed in this way. The occasional uniparental female of *M. hebetor* developed from tetraploid eggs in which meiosis was normal, and which probably originated in patches of tetraploid tissue in the ovary.

Since tetraploidy is usually accompanied by a reduction in number of cells, a relatively low ovipositing capacity would be expected in females producing type-I eggs. The uniparental race of *Diprion polytomum* has a much lower reproductive capacity than has the biparental race (Smith, 1941). Smith, however, was unable to distinguish any polyploid nuclei in the germinal cells of *D. polytomum*, although he found them to be numerous in the somatic tissues.

According to Smith (1941), the amount of chromatin material in the oogonia of the uniparental race of *Diprion polytomum* exceeds that of the biparental race by only 2 chromosomes, there being 14 chromosomes in the uniparental race and 12 in the biparental race. In both races meiosis is apparently normal, but in the uniparental race Smith considered chromosome reduction to be compensated for by refusion of the second polar body with the female pronucleus.

On the other hand, the type-I eggs in the uniparental sawfly *Thrinax macula* are said to remain diploid by undergoing one maturation division (Peacock, 1938).

Tetraploidy of the oogonia, however, seems to be the simplest of the methods by which type-I eggs may be produced, and the one most likely to be brought about by environmental conditions.

It may be significant, from the standpoint of the doubling of the chromosomes in the oogonia, that, with the

cynipid *Dryophanta erinacei,* Triggerson (1914) noted a
larger larval abdomen in the generation destined to pro-
duce type-I eggs than in the generation destined to pro-
duce type-II eggs.   A similar phenomenon occurs in the
case of *Diprion polytomum,* the uniparental race of which
has a higher proportion of large individuals than the
more rapidly developing biparental race.   In insects, the
amount of food consumed during the larval period may
determine, within specific limits, the size of the mature
individual.   However, in the two species cited, the mor-
phological differences between the uniparental and bi-
parental forms, probably induced by the *quality* of the
food rather than by the amount, are instances of dimorph-
ism.

Brues (1928) suggests that with *Pelecinus polyturator,*
the female of the supposedly uniparental race inhabiting
temperate North America is tetraploid, since it is so
much larger than the female of the supposedly biparental
race inhabiting tropical America.

An ovarian dimorphism in the Hymenoptera is indi-
cated by the occurrence of egg types I and II.   An ovary
is either arrhenotokous (all eggs diploid), thelyotokous
(all eggs tetraploid), or amphitokous (eggs tetraploid
and diploid).   When the uniparental offspring of a
female consist of equal numbers of males and females,
it is quite possible that one ovary is thelyotokous and the
other arrhenotokous.

Influence of Environment in Determining Type of Ovary

Observations on the sexuality of the broods of *Habro-
lepis rouxi,* when parasitic in red scale (an unnatural
host), indicate that one type of ovary may be converted
into another type if the developing larva is subjected for
a period to certain nutritional conditions which are not
optimum for reproduction.

Qualitative differences in nutrition are known to be
the cause of dimorphism in certain Hymenoptera (Salt,
1937; Schmieder, 1933).   It is significant that the hymen-

opterous ovary is a plastic organ which reacts to trophic stimuli (Wheeler, 1928). The number of ovarioles in the adult may be determined by the nutrition of its early larval stages. It is well known that, in the social Hymenoptera, morphological and physiological differences exhibited by the ovaries of workers and queens result from differences in larval nutrition. Such differences may initiate differences in rates of development and thus have a dimorphic effect (Power and Melampy, 1943). When the worker appropriates for itself food that ordinarily would be fed to larvae selected to become queens, its rudimentary ovaries undergo development and it becomes capable of depositing unfertilized eggs. Whether such eggs develop into males or into females, as in the Cape honeybee (Jack, 1917), also may depend on nutrition.

Experiments with Habrolepis rouxi. This is an endoparasitic uniparental species whose development is readily affected by the kind of plant, or by the condition of the plant, fed upon by its host (Flanders, 1942b). During the several years when mass production of *H. rouxi* was being carried on in the insectary at the University of California Citrus Experiment Station, it was noted that the sexuality of the parasite populations seemed to be affected by the type of host plant used. Reproduction on squash fruits resulted in a higher proportion of males than reproduction on lemon fruits (Flanders, 1942a). A similar difference was noted in parasite populations reared from red scale on freshly picked grapefruit and from red scale on old grapefruit—that is, grapefruit held for 30 days at 80° F. Significantly, the viability of red scale is noticeably less on old grapefruit than on fresh grapefruit.

The sexuality of populations of *Habrolepis rouxi* also seemed to be affected by the maturity of the insect host, a higher proportion of males occurring when the red-scale host was immature than when it was mature. A complicating factor was a tendency toward male production seemingly correlated with high temperatures, males

being relatively more numerous in summer than in winter. A series of experiments was therefore undertaken to determine the relative effects of host plant, maturity of insect host, and environmental temperature on the occurrence of males.[6]

Red scales between 35 and 55 days old, when grown at a constant temperature of about 80° F, are most suitable for the development of *Habrolepis rouxi*. Scales less than 20 days old are least suitable, for in such scales development of the parasite is considerably prolonged. Suitability increases with the age of the scale, up to about 35 days, and is probably an effect of chemical differences.

In preliminary tests using groups of female parasites, 24 females reared in red scale over 35 days old and *equal in maturity* were all thelyotokous, for they had 667 progeny, all of which were female. The progeny of 16 females reared in young scale (16 to 27 days old when attacked) consisted of 172 females and 9 males, while the progeny of 16 females reared from nearly mature scale (26 to 36 days old when attacked) consisted of 243 females and 5 males. The progeny of each group were reared in scales of equal age, on lemons, at 80° F.

The data in Table I, based on the broods of 91 isolated females, indicate that the temperature during the development of the female accentuates the effect of nutrition on the sexuality of its brood. In most cases the broods were incomplete because the parents were allowed to oviposit for only about 20 days. At 80° F, the life of the ovipositing adult may be as long as 40 days. However, as noted previously, the sexuality of a brood is apparent soon after emergence begins.

As Wigglesworth (1939) has stated, growth, or reproduction, or some other function, may be adversely affected toward the limits of the temperature range of the species. In the case of *Habrolepis rouxi*, if the entire larval growth takes place at 90° F, pupation is inhibited unless the tem-

[6] The experimental data obtained in the reproduction of *Habrolepis rouxi* were collected, under the writer's supervision, by Glenn L. Finney, superintendent of the insectary, whose assistance greatly facilitated this study.

perature is lowered. But pupation at 90° F is not in-
hibited if exposure to this temperature does not occur
until after larval feeding ceases. Under optimum con-
ditions for maximum reproduction, all females are thely-
otokous. Females that develop in immature hosts on
fresh grapefruit, or in mature hosts on old grapefruit,

TABLE I

Types of Ovaries, as Determined by the Sexuality of the Broods, of 91
Females of Habrolepis rouxi, Correlated with Certain Environ-
mental Conditions to Which the Female Parasites were
Subjected During the Early Stages of their
Development

Test	Age (in days) of red scale* when exposed to female parasites	Host plant	Temperature (degrees Fahrenheit) during developmental stages of female parasites	Females grouped according to ovarian types†		
				Thelyotokous	Amphitokous‡	Arrhenotokous
A	17+	Squash	80°	14	1	
B	27+	Fresh grapefruit	68°–73°	8	2	
C	28	" "	80° (larval stage, 90°)	2	2	
D	27	" "	80° (early embryonic stage through larval stage, 90°)		8	
E	27	" "	80° (early embryonic stage through first half of lar- val stage, 90°)	3	6	1§
F	34+	" "	80°	6	1	
G	39	Old grapefruit¶	70°–73°	8		
H	39	" "	80°	9		
I	39	" "	80° (embryonic stage, 90°)	8	2	
J	39	" "	80° (early embryonic stage through first half of lar- val stage, 90°)	1	6	3

* Red scale in this experiment were mature when about 38 days old.
† The offspring of the 91 female parasites (2,548 females and 384 males) were reared in red scale on grapefruit, at a constant temperature of about 80° F. The type of ovary apparently had no influence on the average number of offspring per female.
‡ The ratio of males to females from amphitokous ovaries ranged from 1 : 46 to 21 : 26.
§ This female had 71 male offspring.
¶ By "Old grapefruit" is meant fruits held for 30 days at 80° F before infesta- tion with red scale.

may be amphitokous. In either case, however, subjec-
tion to high temperature is necessary to cause these fe-
males to become arrhenotokous.

Developmental temperatures alone do not determine the
bisexuality of uniparental populations. Numerous tests
with the biparental species *Mormoniella vitripennis* by
Moursi (1943), and with *Microbracon hebetor* by the

writer, using low temperatures, have failed to yield uniparental females.   The writer also subjected numerous individuals of the uniparental species *Nemeritis canescens* Grav. to high temperatures during development without bringing about the production of males.

Prebble (1941) has called attention to the fact that the unisexuality of the uniparental race of *Diprion polytomum* is correlated with the occurrence of diapause, and that bisexuality is correlated with the lack of diapause. This correlation indicates that hormone activity may be the nutritional factor involved in the dimorphism of the ovaries.   "Diapause" generations may alternate with "nondiapause" generations, the diapause being determined long before it becomes apparent.   It is of interest to note in this connection that silkworm eggs incubated at 25° C (77° F) tend to produce moths that deposit "diapause" eggs, while those incubated below 15° C (59° F) tend to produce moths that deposit "nondiapause" eggs (Wigglesworth, 1939).

Biparental and Uniparental Reproduction as a Facultative Phenomenon

In the biparental reproduction of females and the uniparental production of males, Dobzhansky (1941) points out (1) that there may be freedom to form gene combinations although the supply of hereditary variations is limited, and (2) that functional haploid males provide a means for the rapid elimination of unfavorable mutant genes, if the genes that are recessive in females have similar phenotypic effects in both sexes.

A species in which the reproduction of females is entirely uniparental may be in a phylogenetic "blind alley."   Peacock (1925) points out that in the Tenthredinidae (sawflies), a group in which uniparental reproduction is of long standing, there is a stereotypy of form. It is not unlikely, however, that a uniparental species subjected to a change in environmental resistance may produce a biparental race, provided the mating instinct is activated.   Conversely, a biparental species subjected

to certain environmental conditions may produce a uniparental race.

The fact that Kelly and Urbahns (Webster and Phillips, 1912) obtained from the biparental species *Lysiphlebus testaceipes* a line of uniparental females which was maintained for two generations indicates that such reproduction is facultative. Kelly and Urbahns suggested that such uniparental reproduction might be an adaptation for carrying the parasite through periods of host scarcity.

No observations have as yet been made on the occurrence of biparental females in a uniparental species, since recognition of such females depends on the occurrence of a difference in form or in chromosome number.

The adults of the uniparental and biparental races of *Diprion polytomum* differ morphologically and in chromosome number. Since the females of the uniparental race have exhibited the mating instinct, there is a possibility that a biparental line may be produced from the uniparental race. A uniparental female with the morphological characteristics of the uniparental race was produced by the biparental race (Smith, 1941). When this occurred, it was assumed that there had been an accidental mixture of breeding stock. It is possible, however, that this female was derived from a type-I egg.

According to Whiting (1943), biparental reproduction with haploid males must have been attained very early in the evolutionary history of the Hymenoptera. Uniparental reproduction in this order would therefore be secondary. The fact, however, that uniparental reproduction appears to be relatively more common in the primitive Hymenoptera than in the higher forms, such as the serphoids, indicates that uniparental reproduction in the Hymenoptera was derived directly from biparental reproduction in which the males were diploid, and not from biparental reproduction in which the males were haploid.

Summary

In the Hymenoptera, the uniparental production of fe-

males is a fairly common phenomenon. All normal males appear to be uniparental.

The species of this order fall into two groups: (1) those species which generally reproduce biparentally, commonly producing uniparental males and occasionally producing uniparental females; and (2) those species which reproduce uniparentally, but with only the occasional production of males, although certain females of this group may produce only male progeny. The occurrence of the different types of reproduction appears to be dependent on a dimorphic condition of the ovaries—that is, ovaries that are either thelyotokous or arrhenotokous.

The life histories of certain species of uniparental Hymenoptera recorded in the literature, and data from observations on the reproduction of the red-scale parasite *Habrolepis rouxi*, indicate that the gonads of the immature female larva, which are potentially thelyotokous, may develop into ovaries that are partly or completely arrhenotokous. This change may result from a change in the nutrition of the larva, accompanied by a change in environmental temperature. It is significant that, in the species noted, the thelyotokous condition is associated with relatively low temperatures, and the arrhenotokous condition with high temperatures.

Observations on *Habrolepis rouxi* indicate that thelyotoky in the Hymenoptera does not necessarily involve a modification of the meiotic process. Thelyotoky commonly may result from a doubling of the chromosomes in the primary oogonia.

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THE RELATION BETWEEN HEREDITY, SEXUAL ACTIVITY AND TRAINING TO DOMINANCE–SUBORDINATION IN GAME COCKS[1,2]

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ALLEE (1942) and Allee and Collias (1940) have studied environmental and hormonal factors in relation to dominance-subordination patterns in vertebrates, and Murchison (1935a, 1935b, 1935c) and Guhl (1942), who also studied domination-subordination, used the discrimination cage for investigating social discriminations in domestic varieties of chickens. In the experiments to be described, especial attention was given to factors which are of significance in the development of dominance in game cocks.[3] The scarcity of knowledge in regard to development of dominance in this interesting and least understood breed of chickens makes additional information about the behavior pattern highly desirable.

MATERIAL AND METHODS

Game cocks used for experimentation were obtained by crossing Allen Roundhead hens with an Arkansas Traveller cock, and the hens obtained were back-crossed with the Arkansas Traveller. Some of the first-generation cocks were used, but their behavior was found to be essentially the same as that of the second generation cocks. In some experiments, behavior in first- and second-generation cocks was checked against behavior in adult Dominique, White and Allen Roundhead game cocks. Hybrid Brown Leghorn, Rhode Island Red, Brown Leg-

[1] All observations were made at Decatur, Alabama, prior to 1923.

[2] The author is indebted to Dr. A. M. Moll, Grand Rapids, Mich., and Mr. J. A. Davidson, Poultry Department, Michigan State College, for reading the manuscript and for valuable criticisms.

[3] Moll states (personal communication) that "true gameness is a recessive characteristic." He adds "some cross-bred cocks (cocks obtained by crossing games with other breeds of chickens) fight fiercely, and are apt to be mean, i.e., they will attack man and other animals."

horn and Barred Plymouth Rock cocks were used in other experiments.

All game chickens used in the experiments were bred and hatched in an enclosure which is described in Fig. 1 as a breeding pen. It consisted of a small house and an attached yard, about 16 feet wide and 20 feet long, fenced
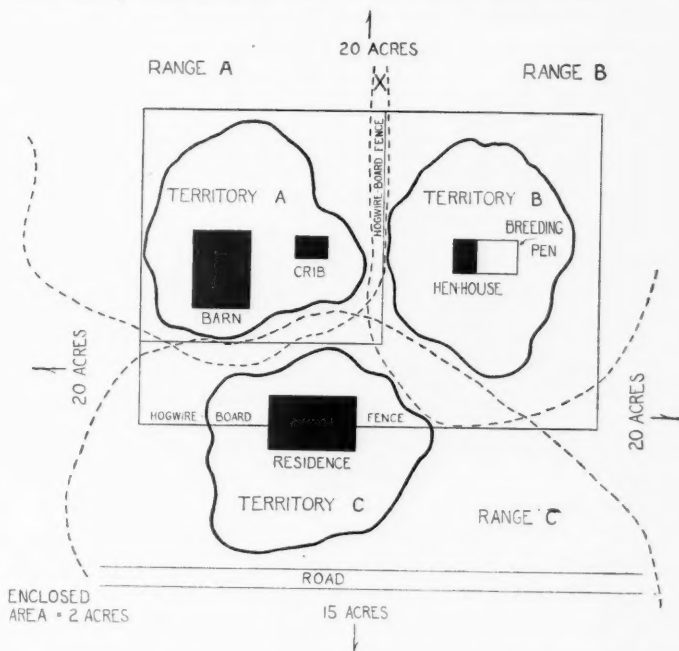

FIG. 1. A diagram showing the relations between territories and ranges. The term, "walk," as used in the text, refers to a territory and the range adjacent to it.

with poultry wire about 60 inches high. The wings of all game chickens were clipped before the chickens were left in the breeding pen. Other fences described in Fig. 1 as hogwire and board fences were constructed from 32-inch heavy fenestrated wire and 6-inch boards. In this type of fence, the lower surface of the wire was in contact with the ground and the upper surface was 6 inches below the lower member of two parallel boards that were spaced

about 6 inches apart. All chickens other than the games were bred and reared on the walks shown in Fig. 1.

In all experiments in which trained cocks were used, the cocks were trained on top of a table (4 feet wide, 6 feet long and 4 feet high), which was covered by a layer of cotton one-fourth inch thick. The following method was used in training: A cock was put on top of the table, and the trainer's hands were placed over or beneath the cock's wings. The cock was exercised by pushing the bird to the left and then to the right for 5 to 10 minutes. Other muscles were exercised by pushing the cock backward and forward for an additional 5 to 10 minutes. Wing muscles were strengthened by releasing the cock 2 feet above the table top; this procedure was repeated for 5 to 10 minutes. Birds in training were kept in small individual pens, and care was taken to keep a cock away from other cocks until the training was completed. The length of the training period depends on the physiological condition of the cock at the beginning of the training period, but with most cocks 2 to 3 weeks was usually adequate. A cock in good physical condition had a well-developed muscular system and showed little fatigue at the conclusion of a training period.

Fig. 1 shows that the breeding yard was divided into territories and ranges. A territory and the range adjacent to it will be referred to in this paper as a walk. Each of the walks, which was surrounded by a supplemental range of 15 or more acres, was occupied by a game cock and 15 to 20 hybrid hens.

OBSERVATIONS

The Relation Between Heredity and Dominance. The relation between heredity and dominance was studied by matching dominant game cocks with dominant hybrid cocks (Rhode Island Red, Brown Leghorn and Barred Plymouth Rock Hybrids), and carefully noting the behavior of each while the matches were in progress. One example will be used to illustrate the importance of

heredity in dominance-subordination. Walk C had been dominated by a large hybrid Brown Leghorn cock for several years. This bird was matched on walk C with a dominant untrained game cock by releasing the game cock at a distance of about 30 feet from the Leghorn hybrid. Both cocks crowed, and the game moved in and hit the Leghorn with both spurs. After about 10 minutes in which the action was fast, it was seen that the Leghorn was tiring. The game continued to carry the attack to the Leghorn, and the Leghorn fought back defensively, but during the match the Leghorn gave way to the game. In one of the encounters made late in the match, in which each cock was the recipient of several blows, the spur of the game broke the skin beneath the eye of the Leghorn, and then the Leghorn discontinued the fight and ran. Both the Leghorn and the game were left on the walk and encounters between the two cocks were frequently observed, but the matches were invariably terminated by the Leghorn. In this match and in other matches between games and domestic varieties of cocks, it was observed that the games tolerated more punishment, and that they were shiftier, faster and less clumsy than domestic cocks. Such marked differences in behavior were doubtless dependent on the hereditary background of the cocks.

Some observations suggested that methods of attack used by some varieties of game cocks may be hereditary. Kentucky Dominique cocks, in most matches, were above opponents before striking, and as a consequence, the Dominiques did more flying in matches than the Allen Roundhead. Roundheads moved to within striking distance and then struck forward or toward either side of opponents. When the Roundhead directed the attack toward the right or left side of an opponent, the legs and feet were brought forward in a sweeping motion so that spur points hit their opponent's body. If opposing cocks eluded their Roundhead opponents by flying upward, the Roundheads were sometimes successful in changing the direction of blows, so that the tips of their spurs hit the

ventral body surface of opposing cocks. At the comple-
tion of such maneuvers, the Roundheads were frequently
lying on their backs, with both legs extended upward.
The high, flying type of attack, as used by the Dominiques
and the shifty, ground attack, used by the Roundheads,
appear to be independent of training.

*The Relation Between Isolation, Sexual Activity and
Dominance.* Game cocks were subordinated by raising
game chicks from hatching time to sexual maturity on
walks with dominant game cocks. A cock subordinated
in this way, when approached by the dominant cock,
would run and remain at a distance that made escape
possible without engaging the dominant cock. While
making these observations, the author noted that sub-
ordinated cocks tread fewer hens than dominant ones.
Such a behavior pattern in subordinated birds may be due
to a decreased sexual activity or to the hens' preference
for dominant males, although Guhl (1942) considering the
same question states (p. 137): "The fact that the social
discrimination of males by females is significant does not
necessarily imply that the hens showed a 'preference' for
l as the dominant male, as their reactions may have been
negative discriminations of ll and lll and positive only
to l."

Some observations suggest that isolation and sexual
activity are important factors in the development of
dominance in game cocks. Only one experiment will be
described which is in support of this view, although the
observations were repeated on many subordinated cocks.
An 11-month-old game cock, subordinated to a cock on
walk A, was removed from the walk, and left on a nearby
farm with 15 or more hens for 3 months. Occasional
observations were made on this individual, and it was
found that the behavior pattern changed from that of a
subordinated bird to that of a more dominant one.

This change in behavior pattern was characterized by
an increase in frequency of crowing, while increased
sexual activity was suggested by the increase in the num-

ber of hens trod. When the young cock was first left at the farm, it appeared as though he were trying to make himself as inconspicuous as possible, but after 4 weeks on the farm, he had straightened and his posture resembled that of a dominant bird. Two months after these observations were made, the young cock was returned, to ascertain whether increased sexual activity and isolation with a strange flock of hens had developed superficial[4] or real dominance. To make a reliable test, the young cock was matched with the cock on walk A to which he had been subordinated 11 months previously. On sight of the cock on walk A, he vigorously attacked the older cock and continued the attack until both were exhausted. These observations and other observations made on subordinated cocks suggest that sexual activity[5] and isolation are important factors in the development of dominance in subordinated birds.

Territories and Ranges of Game Cocks. Allee (1942) states (p. 143): "All group organizations among birds are apparently based on the ability of birds to recognize and remember their flock-mates as individuals. When territory enters as a factor, recognition of the individual's territory also becomes a part of the group reaction system."

To obtain a more accurate understanding of recognition of territory and of individuals by game cocks, it was found expedient to divide walks shown in Fig. 1 into territories and ranges. Each division is used in the same sense as it was used for small mammals by Burt (1940). He defines a territory as an area around a home-site, defended against members of the same species, while a home range is an area adjacent to a territory not necessarily defended, which is used for foraging.

Several years later (1943, p. 351) this author states: "Home range then is the area, usually around a home-

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[4] An individual exhibiting superficial dominance when matched with a true dominant will discontinue the match after a few minutes of fighting.

[5] According to Moll, sexual activity is not necessary for the development of dominance. Isolation is just as effective as isolation and sexual activity.

site, over which the animal normally travels in search of food.   Territory is the protected part of the home range, be it the entire home range or only the nest.   Every kind of mammal may be said to have a home range, stationary or shifting.   Only those that protect some part of the home range, by fighting or aggressive gestures, from others of their kind, during some phase of their lives, may be said to have territories.''

It was found during the course of these observations that cocks usually remained within boundaries of their respective walks.   On occasions, cocks would enter ranges of adjacent walks, *i.e.*, at feeding time or while foraging. Territories, however, were always respected.   This is well illustrated by the following observations: Cock A and hens frequently foraged on range A at a distance of 100 yards from territory A and at such times cocks B and C did not trespass on territory A.   Under these conditions, recognition of territory by B and C may be similar to the mammalian conditioned reflex.   If this is the case, both the individual and the individual's territory were concerned with territorial recognition.   Moll states (personal communication) that territorial recognition was abolished in a game cock when hens were removed from his walk.   When this was done the cock fought it out with the cock in an adjacent walk for domination of the flock in the adjacent walk.   This would indicate that the presence of hens on a walk was a limiting factor in territorial recognition.

When cocks were foraging on ranges, some distance from their respective territories, recognition was made of the individual.   This was well illustrated by the following observation: It was noted that cock B and hens frequently foraged at X (Fig. 1), an area frequented by cocks B and A.   When X was occupied by B and hens, and A and hens moved toward X, the presence of both cocks was soon established by crowing.   Cock B and hens continued to forage, although the foraging course was altered by B moving to the right into range B.   Likewise,

cock A and hens continued to forage, but moved to the left into range A.   Neither cock made any pretense of defending the range at X.

Fights between dominant cocks rarely occurred, as walks were large enough to decrease the frequency of unavoidable meetings of cocks while foraging.   Sexual competition between cocks was at a minimum as each walk was supplied with 15 or more hens.   Cocks B and C occupied their respective walks for over 12 months, and in this period fights which were dependent on the individual initiative of one or both cocks were never observed.   Thus, the contention of Noble (1939) "that no two hens, or roosters can remain very long together in the barnyard without establishing which is superior to the other" is acceptable only when applied to a barnyard of a limited area.

The Relation Between Dominance and Training.   In a study of the relation of behavior to training, cocks were trained as described in the preceding pages.   A cock, when returned after training to the walk which he had occupied prior to training, usually established his presence by crowing and beating the wings against the body. If the trained cock observed another cock on an adjacent walk, he usually moved into the adjacent walk to attack. A trained cock, when taken into the territory of another cock and then released, would aggressively attack the dominant cock in the territory.   Action in matches made under either of these conditions was fast, and the trained bird continued to carry the attack to the opponent.   As the match progressed, the effects of training were evident. The trained cock was shiftier, showed less fatigue, and also gave the impression of being a superior fighter.   In matches made between trained and untrained game cocks, care was taken to match cocks of about the same age and weight, so that differences in behavior observed while the match was in progress could be more closely correlated with training.   The observations described in the preceding paragraph suggest that training was an important

factor in developing aggressiveness and stamina in game cocks, and that increased aggressiveness and stamina, under the conditions described, may be closely correlated with dominance.

Discussion

Scott (1942) finds that in sage grouse, the social organization on mating spots consists of a central group of hens, a master cock which dominates the group, a sub-cock or chief rival cock and several guard cocks. Master cocks are aggressive, vigorous and usually larger than other cocks in the organization. This author also found that master cocks always mated a greater number of times than sub-cocks or guard cocks. If it is assumed that increased frequency of mating in sage grouse is correlated with increased sexual activity, the development of dominance in sage grouse cocks and game cocks is fundamentally the same. It was suggested in the preceding pages that training increases aggressiveness and stamina in game cocks, and that both aggressiveness and stamina seem to be important factors for the development of dominance in grouse. A further comparison of dominance in game cocks and sage grouse cocks shows that the behavior of sage grouse guard cocks and young subordinated game cocks is similar in several respects. Both recognize and accept the dominance of other cocks, and in this acceptance guard cocks remain outside the breeding spots during the mating season; consequently, such cocks mate only occasionally. Likewise, subordinated game cocks remain in the outskirts of a walk, some distance from the flock, and mate when the vigilance of the dominant cock slackens. Master cocks dominate grouse social organizations by threatening and fighting, and domination of a walk by a game cock is maintained by essentially the same methods.

It is evident that a comparison of social organization and dominance in grouse and game chickens should be used with considerable reservation as this method, if carried to the extreme, may yield false conclusions. This

comparison in no way constitutes proof that social organization is essentially the same in both sage grouse and game chickens, and it is offered with the idea that such comparisons may give clues to investigations which may further elucidate the biological and environmental factors that determine the avian behavior pattern.

Summary and Conclusions

Observations made on game chickens, on walks with an area of one or more acres, suggest that dominance-subordination and social organizations are determined by factors which on final analysis are closely related to the hereditary background of the individual. Courage, aggressiveness and shiftiness, all of which are important in domination-subordination, are hereditary, as these characteristics are exhibited to a greater degree in games than in the common domestic fowls considered. Other factors, such as training, isolation and sexual activity, aid in the expression of these latent hereditary characteristics. The results also suggest that identical environmental factors exert less effect in directing the behavior pattern toward dominance in other breeds of chickens considered than in game chickens.

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"NICKING" IN RELATION TO SEXUAL
MATURITY OF S. C. W. LEGHORNS[1]

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THE concept of nicking is widely accepted among poultry and animal breeders. In general the term "nicking" is used in reference to matings which are particularly successful by the quality of offspring produced. More specifically, if the progeny of a pair of given parents is superior to that expected by the breeder on the basis of his estimates of the genotypes[2] of the sire and dam, usually from their phenotypes, the mating is said to have nicked well. The consequences of the belief in the existence of this phenomenon have not been particularly emphasized in the past. Yet its implications are rather far-reaching, since, should nicking be of frequent occurrence, it would mean that the results of a progeny test must be taken to refer to the particular combination of parents rather than to the sire and dam individually. In such a case the death or incapacitation of one of the mates (particularly of the sire) would demote the other from the status of a proven breeding bird and require its retesting with a new mate. On the other hand, should nicking be non-existent or unimportant, once a bird has had a successful progeny test with one mate, its genotypic worth may be considered established.

From the genetic point of view the term "nicking" may be considered to be due to two different phenomena: (1) gene interaction of the complementary, epistatic or generally non-additive type, and (2) character interaction. In the final analysis such distinction is undoubtedly arbitrary, but from the standpoint of actual breeding practise it is of importance to consider the two types sepa-

[2] The terms genotype and genotypic are used here, unless otherwise specified, to designate all hereditary effects including non-additive ones.

rately. The first is probably the one more familiarly used in reference to characters not broken down into component factors. The second, referred to by Richey (1942) as "mock-dominance," is well illustrated by the inbred tomato lines cited by Powers (1944), where a cross between one line with a small number of fruits of large weight and another line characterized by many small fruits produced a greater total yield (number of fruit $\times$ average weight of fruit) than either parent.

An analogous situation may be imagined with respect to egg production in chickens, which can be considered as the expression of interaction of several independently determined characters (Lerner and Taylor, 1943). Thus should a late maturing line with a high rate of production be crossed with an early maturing but low-rate line, it would be reasonable to expect the total number of eggs laid by the progeny of such a cross to exceed the records of the parents. This situation in a certain sense is not nicking at all, since additive gene action alone could lead to it, and since the superior results from the cross would be predictable by the breeder in possession of information on the component characters as well as on the total yield of the parental lines.

The first type, that of gene interaction, may in some cases resolve itself into character interaction, should a breakdown into component factors be made. However, in many cases the breeder may be dealing with characters which can not be broken down any farther either because they are the direct result of gene action or (which is certainly more likely the case with economic characters) because of our incomplete knowledge of the physiology of their development. Some of the components of egg production (Lerner and Taylor, *loc. cit.*) belong to this category, and may then be examined for the existence of the nicking phenomenon.

The amount of data necessary to distinguish nicking from sampling deviations is considerable, and special experimental designs would be highly desirable to achieve

this purpose. Some information, however, may be obtained from records already available. Thus it was found that the necessary data were at hand for the character of sexual maturity, since sufficiently large numbers of offspring from each mating were measured for this character before mortality reduced them to numbers too low for the intended purpose.

Design of Analysis

In the mating records of the University of California flock of Single Comb White Leghorns a series of 31 diallel sets of matings (that is to say, where two dams have been mated at different times to each of two males), producing an adequate number of female offspring, has been located. In five of these sets the mated group contained three dams, and in one case four dams. Thus the total number of sires involved was 62 (31×2), while the number of dams included in the study was 69 ($25 \times 2 + 5 \times 3 + 1 \times 4$). Discounting duplication of the same individuals in different sets, the number of sires was 49 and that of dams 64. In each set the number of pullets, for which the age at first egg (the usual criterion of sexual maturity) was available in the smallest full-sister family, determined the number of pullets selected for study. Thus in a set where the four full-sister families had respectively 3, 5, 5 and 8 birds, three pullets of each family were selected by means of a table of random numbers, or 12 pullets for the set as a whole. Since the population was not culled at any time prior to the beginning of laying, the pullets may be considered to represent a random sample of the matings analyzed. Of the 31 sets, 13 had 3 pullets per family, 7 had 4, 10 had 5, and 1 had 6, involving a total of 548 pullets. Thus while the number of birds varied between sets, within each set the number per family was constant.

This characteristic of the data permitted the carrying out of analyses of variance within each set so that the total variance could be partitioned into four parts: (1) due to differences between sires, (2) due to differences

between dams, (3) interaction, and (4) error. The first
of these unfortunately represents not only the genetic
contribution of the sire to the character of the daughters,
but also the inter-year variability, since the two are per-
force confounded in this design. The second provides a
measure of the dam's contribution, although should per-
sistent maternal effects exist they would be included in
this portion of the variance. Outside of the unlikelihood
of such a situation such an eventuality would only lead
to an overestimate of the dam's genetic contribution to
the daughters, but not affect the primary problem, that
of nicking. The existence of the latter can be detected
by the magnitude and statistical significance of the third
of the listed sources of variance.

An additional point needs to be mentioned, and that is
the fact that some of the sets include matings between
individuals from populations not interbred for several
generations. These matings were made in various in-
heritance studies in which the F_1 birds were eventually
discarded without having reproduced themselves. Such
sets would obviously have a greater likelihood of exhibit-
ing nicking than sets derived exclusively from freely in-
terbreeding populations.

RESULTS

As already stated the magnitude of the interaction in
excess of the errors in the above described analyses of
variance may be taken as a measure of the import of non-
additive action or more specifically of nicking. The rela-
tively small number of birds in each set of data may be
a limiting factor in the verification of the statistical valid-
ity of any interactions present. It is possible to circum-
vent this difficulty by obtaining a pooled estimate for all
the sets of matings studied, provided their variances are
homogeneous. A somewhat similar block design has been
used by Lush and Molln (1942) in analyzing litter size in
swine. A simple test for homogeneity has been proposed
by Bartlett (1937) and applied to data at hand in accord-

ance with the procedure outlined by Roessler (1943). The χ^2 for the 31 sets with 30 degrees of freedom was found to be of a magnitude (67.49) indicating some amount of heterogeneity between the sets. Examination of the values contributed by each of the sets to this χ^2 revealed three sets to be responsible for a large share of it. When these three sets were eliminated the recomputed χ^2, for 27 degrees of freedom was found to be 31.83, corresponding to a P point in the neighborhood of 0.25. Thus the 28 remaining sets may be considered to have homogeneous variances permitting valid pooling, while the data for the other three sets may be considered separately.

TABLE 1

POOLED VARIANCE OF HOMOGENEOUS MATINGS

	Total	Between sires	Between dams	Inter- action	Error
Degrees of freedom	464	28	35	35	366
Mean square	598	1974	921	498	471
Percentage of variance ..	100.0	24.2	7.6	0.9	67.3
F		3.96	1.85	1.06	

Table 1 presents the pooled variance due to each of the indicated sources and clearly shows that no significant interaction is present in the material at hand; or in other words that nicking does not play an important part in the determination of sexual maturity. This is further confirmed by the fact that none of the contributing sets, whatever their origin, had interactions that were of significance. The variances of the three sets that were not used for the pooled estimate are presented in Table 2. It is clear from the readily computable variance ratios that nicking is of no greater significance in these matings than in the other 28 sets.

To the knowledge of the writer only one previous analysis of nicking in animals with results capable of statistical verification has been presented. Seath and Lush (1940) by a different method reached the conclusion that nicking is of little importance in the inheritance of both milk yield and butterfat percentage in dairy

cattle. Attention must also be drawn to their *a priori*
arguments against any widespread effect of epistatic
deviations. The data presented in this paper bear out
this point of view (though it should be noted that con-
trary argumentation has also been reviewed by Seath and
Lush). It is of course, impossible to generalize from
these results to other characters, but with respect to this
population, it may be asserted with some confidence that
epistatic deviations play no important rôle in the deter-
mination of sexual maturity. Consequently, once a breed-
ing bird has been proven with one mate or a series of
mates, it may be considered to possess genotypic quali-
ties desirable in whatever mating it is used.

TABLE 2

VARIANCE OF MATINGS CONTRIBUTING TO THE HETEROGENEITY OF POOLED DATA

Set number		12	15	18
Total	degrees of freedom	11	19	23
	Variance	1,512	3,483	1,653
Between sire means	degrees of freedom	1	1	1
	Variance	2,324	22,178	1,219
Between dam means	degrees of freedom	1	1	1
	Variance	19	12,694	950
Interaction	degrees of freedom	1	1	1
	Variance	126	6,193	425
Error	degrees of freedom	8	16	20
	Variance	1,771	1,570	1,771

Reference should be made here to an investigation of
a similar problem in corn by Sprague and Tatum (1942),
who found that in unselected material differences between
lines were largely due to additive effects of genes ("gen-
eral combining ability"), while nicking ("specific com-
bining ability") was of no relative importance. How-
ever, in crosses between lines already selected for high
general combining ability, non-additive or nicking effects
assumed a much greater rôle. The process of selection
resulted here in the elimination of the differences in addi-
tive effects between lines, so that specific combining ability
became responsible for the major proportion of the genetic
differences between the selected lines. Presumably the
same situation may arise in the case of sexual maturity
in poultry, should internally homogeneous lines similar to

each other in phenotype but differing in genotypes be established.

ESTIMATES OF INDIVIDUAL HERITABILITY

The partitioning of the variances within sets of matings presented in pooled form in Table 1 permits the estimation of the degree of individual heritability of sexual maturity. Previously (Lerner and Taylor, *loc. cit.*) the degree of family heritability (the portion of variance between families of full sisters which is attributable to genetic effects) has been estimated at about 20 per cent. Certain features of the present design referred to in its description place a definite limit on the precision of the estimate possible here. However, a rough appraisal of genetic variability can be made from the intraclass correlations appearing in the form of percentage of variance in Table 1. Assuming the absence of sex-linkage and of non-hereditary maternal effects, twice the variance attributable to the dam plus that attributable to interaction yields a total heritability of about 16 per cent. On the other hand, if the variances attributable to all sources except the error are added up an estimate of the genetic variance between individuals approaching 33 per cent. is obtained. While the former figure is a definite underestimate in view of the demonstrated sex-linked differentials (Lerner and Taylor, *loc. cit.*), the later is undoubtedly an overestimate, since it includes the variation between years confounded with that between sires. If the purely hypothetical maternal effects are considered to be at the least offset by sex-linked effects the probable limits of individual heritability of sexual maturity are between 16 and 33 per cent., a range covering the previous estimate of family heritability.

SUMMARY

An analysis of diallel matings in a White Leghorn flock indicates that "nicking" or non-additive deviations in general do not play an important part in the determina-

tion of sexual maturity. The individual heritability of
this trait is found to be within the broadly established
limits of 16 to 33 per cent.

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HEAT–INDUCED STERILITY AND ITS POSSIBLE BEARING ON EVOLUTION

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WHEN viewing the events that transpired during the course of evolution as portrayed by the paleontological record, we are confronted by the notable frequency of extinction of families, genera and species, and to a more dramatic extent by the phenomenon of the entire disappearance of many apparently virile and even once dominant faunas. The nearly complete obliteration of the reptiles as represented by the archosaurians, and the failure of many families and genera among the mammals, birds and other animal organisms furnish typical illustrations of these events.

Extinction has been explained as a possible result of orthogenesis culminating in the over-development of harmful traits; more recently it has been explained as a simple accessioning, or accumulation of deleterious mutations, or as being due to racial senescence, or as a result of unaccustomed stresses brought about by any one of several new biotic complications. Changes in climate have been proposed as possible explanations of extinction in certain groups, the most recent one being that of Cowles (1939 and 1940) advocating high temperatures as a possible factor in the case of the late-Cretaceous archosaurians.[1] Wieland (1942) has objected to this view and has proposed that changes in atmospheric carbon dioxide content brought about their demise due to strangulation, resulting from loss of the necessary respiratory stimulant!

Although there is evidence to support some of these

[1] I am greatly indebted to Dr. Edwin H. Colbert, of the American Museum of Natural History, for the only tenable objections to the original heat theory. His objections and my persistent conviction that high temperatures were somehow involved in the phenomenon of extinction led to the present modification of the original theory.

hypotheses, and although several of them, either by themselves or in combination, may have been involved in some instances of extinction, none is completely satisfactory and it seems desirable to call attention to a commonly known characteristic of terrestrial animal organisms that may ultimately lead to the inclusion of another important factor involved in the extinction of faunas and the general process of evolution. At present the evidence is fragmentary, and promises to remain so until attention is directed toward the solution of the many problems that seem to contain the necessary information. These problems are too numerous to be solved in a short time unless many individuals of diversified training can be induced to contribute their knowledge and the results of their studies.

The animal trait that may have played so significant a role in evolution is the susceptibility of the male germ cells, at least during active spermatogenesis, to temperatures above normal for the testis. This temperature response is modified by both intensity and duration of the exposure and produces varying effects on fertility by causing sterility or by diminishing the numbers or viability of sperms. As will be seen, there is also the possibility that high temperatures may be connected with the proliferation of variations.

If the prehistoric terrestrial animals responded to overheating in the same manner as those of today, there can be little objection to the suggestion that testicular susceptibility to supra-normal temperatures might have been a significant factor in the process of evolution. Obviously, there is no direct method by which this can be positively ascertained—therefore only a tentative conclusion can be achieved by the deductive method, and this requires the gathering of pertinent evidence from as many and diversified sources as possible. Nonetheless enough information seems available to provide the general framework necessary for a preliminary exposition of a tentative hypothesis.

A review of the literature provides ample evidence for the statement that heat-induced sterility at the present stage of evolution, is a phenomenon of wide occurrence and that it characterizes every known species of terrestrial animal that has been studied from this standpoint.

Although lowering temperatures to below normal may result in a temporary suppression of spermatogenesis, this appears to be a result of a general reduction of the metabolic rate, and the effects are evanescent. Normal low temperatures are not believed to play a major part in the reproductive processes because of the fact that most, if not all, cold-blooded animal organisms operate at maximum efficiency at thermal levels that are only slightly below the threshold where heat induced damage is inevitable. On the contrary, with the possible exception of the stenothermal warm-blooded animals, the danger point from cold lies well below optimum thermal level (Cowles, *supra cit.*).

The universality of the phenomenon of testicular sensitivity to heat is readily apparent from even a casual survey of the pertinent literature.

Young and Plough (1926) have noted the phenomenon of heat induced sterility in *Drosophila,* while Norris (1932) reports a similar condition in the moth *Ephestia kühniella.*

The effects of cryptorchidism and heat on the mammalian testis were partly surmised at the time that Felizet and Branca (1898 and 1902) called attention to the effects of cryptorchidism in man. Sand (1922) experimented with surgical replacement of the testes and found that degenerative effects resulted, but it was not until the studies of Moore (1924) and Moore and Chase (1923) and the classical work of Moore and Oslund (1924) that heat-induced sterility came to be a widely recognized fact.[2]

[2] Since the writing of this paper, my attention has been called to the report of J. K. Lamar and R. Rogers, 1943, ''Season and Human Fertility in Galveston, Texas.'' (Abstract, *Anat. Rec.,* v. 87, 4) in which it is shown that there is a correlation between low temperatures and the rate of conception. More notable because of the absence of the complicating factor of the psychological

These and other experiments on mammals, such as those of Harrenstein (1928), Young (1929), Phillips and Mc-Kenzie (1934), provide indubitable proof that heating the mammalian testis to above its normal temperature will cause sterility, and that in the scrotal mammals, even normal body temperatures applied to the testis cause its degeneration. These studies, with those of Moore and Quick (1942) have provided unquestionable evidence that the chief physiological function of the scrotum, and testicular migration, is thermoregulatory. The extraordinary significance of these findings in terms of survival and evolution have not been commented upon, possibly because at the time they seemed to represent only an isolated phenomenon.

Riley (1937) has presented strong evidence for the existence of what actually amounts to periodic heat sterility in the English sparrow. In this bird, spermatogenesis is an interrupted process which takes place only when the body temperature falls several degrees below normal in the early morning hours. Under conditions of normal daytime activity, the high body temperature appears to inhibit spermatogenesis. It is probable that this interrupted type of spermatogenesis may have been anticipated by the reptiles.

Witschi (1942) has called attention to the remarkable affects of temperature on the ovo-testis of larval amphibia and while these findings do not constitute direct proof, they do suggest the possible presence of special germinal sensitivity and the need for experimental studies to determine whether or not thermally induced sterility may characterize the adult Salientia. Grobstein (in lit.) states that the testes of *Triturus rivularis* collapse prematurely if the animals are maintained in warm water in the laboratory, whereas under cold conditions they re-

element, is the correlation of high temperatures with the increase in stillbirths resulting from conceptions occurring in July, August and September, which may increase as much as 134 per cent. above the minimum from conception occurring in June. The studies are being continued.

main normal for a longer time. This suggests the possi-
bility that careful investigation will disclose the existence
of gonadal heat collapse in these animals.

Experiments have been completed on one species of
reptile, the only remaining group of terrestrial verte-
brates for which there are apparently no reports on the
sterilizing effects of high temperature. These recently
concluded experiments (Cowles and Burleson, in ms.)
have produced indubitable proof that non-lethal high tem-
peratures (36.5° C.) will cause sterility in the nocturnal
lizard *Xantusia vigilis.*

Pertinent observations on the reproductive habits of
the garter snake *Thamnophis sirtalis sirtalis* have been
recorded (Blanchard and Blanchard, 1942) and the re-
port indicates that these reptiles also may be susceptible
to heat effects since fertile matings do not usually occur
after the onset of hot weather during late spring; that is,
ordinarily not after mid-May. It is therefore highly
significant that a period of cool autumn weather followed
by a libido-stimulating rise in temperature not only re-
sults in renewed matings, but that these are fertile. Ap-
parently even the viable sperms of late spring fail to sur-
vive the summer months, whereas those produced in the
autumn will remain unharmed by the low winter tempera-
tures to which they are subjected.

Although I have been unable to find conclusive reports
on the fishes, there seems to be a strong possibility that
even these non-terrestrial organisms may suffer germinal
impairment by exposure to heat.

From the foregoing review of the effects of high tem-
perature on the male reproductive mechanism of a wide
variety of terrestrial animals, it appears possible that
most representatives of all the Classes of land-dwelling
organisms also may be characterized by the existence of
this curious thermal hiatus. It is particularly notable
that in at least one group, normal temperature require-
ments are greater than can be endured by the spermato-
genic process.

While it may be protested that chance has led to the selection of special cases, actually there is little possibility that the wholly random selection employed in these studies favors an accumulation of artificial evidence. It would seem, on the contrary, that these examples could not have been selected in a less prejudiced manner, and that therefore they should be thoroughly representative of the conditions that we may expect to find in most of the species of classes and orders of land animals.

Although there is no way of knowing whether the ancestral representatives of these orders were characterized by this thermal hiatus (which might be known as thermal divergence or thermal incompatibility) it is highly improbable that so great a diversity of types as those represented in these studies could have developed the trait independently. Certainly it is possible that the existence of the character in living representatives of animals of very diverse nature but having common ancestral origins suggests the possibility of its great antiquity and thus provides us with the tentative basis necessary for the assumption of its phylogenetic spread and continuity over a long period of time.

The circumstances that might result in overheating the body, and thus the testes, most obviously would be a change in climate that would produce either a higher mean temperature throughout the year, or higher mean or maximum temperature during the period of active spermatogenesis. Changes in the relative humidity might possibly lower the efficiency of the cooling mechanism to such a degree as to allow an injurious rise in body temperature, but this appears to be rather less probable than a rise in environmental temperature. Any of these environmental changes presumably would permit the survival of only those forms that became accommodated to the new conditions through successful modification of habits, as by the adoption of nocturnality or migration, or by a change in habitat as, for instance, by retreat underground or to an aquatic environment. It is difficult to

conceive of any of these changes resulting by any means other than the process of mutation channeled by selection through survival.

The problem of higher environmental temperatures might also be met by the development of body cooling devices; sweating, panting, etc.—such as those found in the mammals, or by some analogous device such as the air sacs that almost invest the avian testis. In the absence of effectual body-cooling stratagems, the testes may be separately cooled during spermatogenesis by placement in cooler areas in the abdominal region, or by means of this periodic migration to just beneath the skin or by permanent suspension outside of the body, in a thermoregulatory structure, the scrotum. All these devices are found in the modern mammals.

In the absence of effective temperature protection for the testes, some other expedient may be necessary and it is entirely possible that the almost universal habit of spring mating by temperate zone cold-blooded land animals, and the warm-blooded birds and many of the mammals, may be a contrivance for avoiding the fecundity limiting effects of over-heated germ plasm. Although other ecological factors are undoubtedly involved in the matter of spring breeding they have apparently obscured the possibility that high temperatures may provide at least a partial alternative, or often an entire explanation of the phenomenon. Support for the thesis that spring breeding may often be due to thermal compulsion can be drawn from the studies conducted on the breeding habits of the thirteen lined ground squirrel, *Citellus tridecemliniatus* (Wells, 1935, a and b) and the reproductive habits of the garter snake (*supra cit.*) and other instances of otherwise puzzling seasonal mating behavior. Undoubtedly many other similar examples will be found when investigation is directed toward their discovery.

Although it is entirely possible that in the past there may have been periods of high temperature comparable to the intervals of subnormal thermal conditions that re-

sulted in glaciation, these interludes would not leave such gross and relatively easily interpreted evidence of their occurrence as those which characterize areas subjected to the action of massive ice movements.   Because of the difficulty of the problem of finding geological or other direct evidence of high temperature it is fortunate that no matter how plausible the future evidence may be, it is not necessary to require the establishment of high paleoclimatic temperatures in order to explain how heat damage could have been incurred by male reproductive organs.

The alternative non-environmental changes that might result in heat-induced lowering or fertility are many.   In the habitats of almost all, possibly all, of the cold-blooded organisms, the heat of the sun's unmodified spring and summer radiation is so great that it will kill some of the cold-blooded animals including reptiles in a matter of hours at most, quite commonly in minutes.   This is highly significant since we are now living in an admittedly semi-glacial period rather than an even equable one.   Under the either equable, warm or possibly hot epochs when corals, palms and other supposedly tropical organisms flourished as far north as Alaska and as far south as Tierra del Fuego, our temperate zone might have been considerably warmer than now.   Therefore, judging by the rapidity with which reptiles may be heat-killed now it seems possible to draw the conclusion that although many of the cold-blooded animals have access to temperatures considerably higher than those they are accustomed to utilize, and might be capable of adopting them so far as the body cells and environmental requirements are concerned, they have not been able to do so in part at least because of the limitations imposed upon them primarily by their heat-sensitive germ cells and other associated requirements.

Birds and mammals, receiving most of their heat from metabolic activity, and having fairly effective heat control mechanisms, are not so apt to be subjected to environ-

mental changes as are the so-called cold-bloods, the ecto-
thermic types; nevertheless, the warm-blooded or endo-
thermic animals possess within themselves the capacity
for generating higher than normal temperatures.   Proof
that they frequently do so for short periods is evidenced
by fevers; furthermore, the loss of effective cooling de-
vices, as for instance sweating, or changes in the environ-
ment which would lessen the effectiveness of these mecha-
nisms might also result in the development of high tem-
peratures.   That the body cells can withstand these up-
ward changes within certain limits is well known, as is
the fact that prolonged or very high fevers can produce
at least temporary sterility in man.   In so far as the
mammals are concerned, it is clear that probably most of
them could not adopt even the avian thermal level with-
out danger of serious disturbances or impairment of the
male reproductive processes, that is, unless the change
was accompanied by the necessary succession of muta-
tions that would apparently be needed to produce a com-
pensating increase in the effectiveness of the testicular
cooling mechanism, or which might create some other
coordinating changes.   The effects of over-heating in
birds does not seem to have been studied from this point
of view although there is some encouragement from in-
direct evidence bearing on this problem (Kendeigh and
Baldwin, 1937).

If it can be discovered that there are valid objections
to the preceding suggestions as to how overheating may
have taken place, it still will be necessary to consider the
possible temperature adjustments that must have been
made as the animals passed through the various transi-
tional stages leading from their original aquatic habitats
to their final conquest of the land and their ultimate
triumph over a thermally changing environment.   Cer-
tainly it seems logical to suppose that the emergence of
the vertebrates from water to land must have exposed
them to rather violent changes in insolation and thus have
confronted them with the necessity of solving new ther-
mal problems.

The change from the water-evaporating skin necessary for amphibian respiration, to the dry skin of the more and more water-independent reptiles has certainly resulted in rather drastic upward revisions both of their temperature tolerance and requirements. In a similar manner, the development of fur, feathers and, in some cases, the additional insulation provided by the acquisition of massive layers of hypodermal adipose tissue, together with the appearance of internally produced and conserved heat would have created new thermal hazards. It is curious, in view of its importance, that there are apparently no special sensory nerve endings having the express function of protecting the testes against heat damage.

Each of these radical evolutionary steps must have been accomplished by the development of compensating advances in the toleration of heat by all of the body cells, both somatic and germinal, otherwise overwhelming heat stresses would have been imposed upon both, but especially on the germ cells because of their probably greater susceptibility to heat. It would seem reasonable to suppose that many of the now non-existent forms simply may have failed to make the necessary adjustments, which therefore would mean that the survivors are a product of successful innovations, beneficiaries of fortuitous mutations which happened to take one or more of the only courses of thermal adjustment that would make survival possible.

If the mutational process is accepted as the necessary mechanism for providing the variations requisite for the operations of selection, then these mutations and the accompanying changes would necessarily have had to bring about a simultaneous and coordinated alteration in the temperature tolerance of both the body and the germ cell mechanism, and whatever the reason, this apparently has not been perfected in any of the forms that have been studied. Because of this situation the question naturally arises as to the nature of the difference in heat tolerance

of these two groups of cells; that is, are they mutationally independent of each other?

It would seem from available evidence that the answer to this question is not at hand, although additional studies on thermal divergence may provide the answer. Even if the cells are not independent, the male germ cells nevertheless are more vulnerable than body cells to the effects of excessive heating. This may be because of the nature of the processes involved in maturation of the germ cells; on the other hand, evidence may arise to show that the body and germ cells are in a sense mutationally independent and separate. Whatever the answer may be, it is not necessary to dispose of this problem before it is permissible to consider other aspects of the well established fact of the thermal vulnerability of the male germinal tissue.

One of the most interesting possibilities inherent in thermal divergence of male germ cells results from the advantages accruing to an animal organism whose body cells are capable of operating at the accelerated metabolic rate resulting from higher temperatures. Van't Hoff's law of a doubling of metabolic activity with each 10° C. rise in temperature is pertinent here. Survival of an organism is often dependent on its alertness to danger, and its speed in avoiding predators—similarly the predators themselves profit by reason of slight advantages in speed and alertness. Since higher temperatures accelerate all physiological activity, survival can conceivably depend on this factor as well as on purely morphological adaptations leading to greater speed.

There would seem to be a strong possibility that survival of the body might frequently depend on the small additional margin of speed and alertness that should result from a utilization of a slightly higher body temperature, but that progress in this advance by a species would be penalized or prevented by the thermal limitations imposed by the need for viable male germ cells. If this can be established, it would seem to be a remarkably significant example of such conflicts of interest.

The compromises resulting from the conflict between the advantages accruing to an animal capable of adopting a higher temperature and the attendant diminution in fecundity resulting from the instability of the germ plasm might be an important factor in accelerating the process of evolution. This is especially significant because Plough (1942) has shown that high temperatures may increase the mutation rate in *Drosophila* by five times the normal, and has pointed out the significant increase in the number of lethals which usually accompany mutational changes. In his concluding sentence he says, ''Where mutation is the limiting factor, it may well be that the increased mutation rate at a higher temperature would produce marked increases in evolutionary diversification. It is perhaps this relation of temperature to mutation which determines the greater number of species in tropical areas.''

As has been shown in the papers cited earlier in this discussion, it is clear that there is another, possibly more exaggerated, impact of temperature on an organism; namely through heat produced sterility or at least a reduction in fertility where the exposure is not so great. With these two effects of temperature in mind, there can be little doubt that the necessary number of replacements left by an animal can be drastically diminished by one or the other or both of these heat effects. Whatever the cause of a reduction in fertility, there can be little doubt that the delicate adjustment between degree of fecundity and the required number of offspring necessary for survival of a species at even normal mortality rates, will be seriously disorganized.

It would appear to be an inescapable conclusion that a disruption of normal population balance would reduce intra-specific competition by reducing population pressure. This initial effect might be accentuated still more through the loss of, or damage to, the essential reproductive stimulus inherent in a normal population density. Reduction in population pressure would seem to provide

for an increased play of mutations; i.e., there would be an enlarged scope for individual variation because of an unwonted increase in the amount of available territory and consequent changes in the nature of competitive activity.

Another product of a reduction in population might result in a radical change in the effects of predation, parasitism, and inter-specific competition. In either case it would appear probable that a higher premium would be placed on mutations leading to the production of adaptive changes that would be required as a result of alterations in the limiting and molding effects of population pressure.

Changes such as those mentioned and other concomitant phenomena might result in greater variety of opportunities for a greater variety of appropriate mutations, a highly important condition if *Drosophila* can be taken as exemplifying the effects of heat, either past or present, on rates of mutation.

The sum of these possibilities seems to indicate a theoretical trend toward rapid speciation, possibly accompanied by gradual decline of the original stock, and ultimate extinction or bare survival as a relic fauna. Very high or very suddenly applied temperature stresses would seem to favor outright extinction of one fauna, followed in especially fortunate successful forms by replacement with another group originating from some less specialized ancestral stock.

From the conclusions of Plough (*supra cit.*) regarding the effect of heat as an accelerator of mutations, it would seem reasonable to expect greater plasticity in a stock in which the compromise between body cell versus germ cell temperature requirements was toward the adoption of higher temperatures, while conversely, it would be expected that heat-conservative types, climate permitting, might incline toward stability. While this may be an oversimplified statement of the problem, it may contribute toward an explanation of the multiplicity of species

in the tropics and scarcity of species in cold areas, but it should be noted that this explanation is diametrically opposed to the conventional explanation as presented by Hesse (Hesse, Allee and Schmidt, 1937.)

Many otherwise puzzling biological phenomena can be explained readily on the basis of this hypothesis, or at least it may be said that the phenomena fit into the hypothesis. Some of these problems have been discussed previously in terms of the effects of heat on the somatic cells; i.e., the bodies of the organisms (Cowles, 1940), but in most instances the present modification and elaboration of the original idea is even better suited to the demands of the evidence.

In the original account, such phenomena as extinction of the dinosaurs and possibly other cases of extinction as well, the migration of birds, development of nocturnalism, etc., were tentatively explained as a possible result of the effects of heat on the somatic cells. While these seem better suited to an explanation based on thermal divergence, some of the other phenomena, such as the nature of the circumstances leading to adoption of terrestrial habits by the original land-inhabiting vertebrates, the transformations from amphibian to reptilian types and so forth, might be modified to include the stimulating and accelerating effects of heat on the somatic cells as well as the limiting effects of heat on the germ cells.

It is reasonable to expect the discovery of many instances in which the germ cells will equal the temperature tolerance of their somatic vehicle. The present absence of known instances of thermal harmony is most surprising and is not the least suggestive part of the picture. While discovery of harmonized cellular tolerance will not be "the exception that proves the rule," the occurrence will not invalidate the argument that thermal divergence constitutes an exceedingly important factor in evolution.

SUMMARY

The advantages accruing to an animal having a higher

than normal temperature, in combination with the existence of a limiting heat sensitivity characterizing the male spermatogenic mechanism, has inevitably led to a conflict between interests which may have been resolved by changes in habits, habitat selections, or the development of general body cooling, or specific testicular cooling devices. Failure to solve the conflicting requirements may have led to either actual or virtual extinction. It appears probable that in many instances, there has been some compromise between opposing interests and that only minor heat strains have been incurred. If the effects of heat on *Drosophila* may be taken as an indication of historic thermal response of spermatogenesis characterizing all organisms, at some or all stages of development, we may logically expect that this thermal civil conflict expedited the process of evolution by accelerating the mutational rate.

The extinction of the archosaurians, also extinction of the primitive mammals and many other terrestrial animals, as well as many other phenomena apparently fit this concept of heat as a factor in the process of evolution.

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REVIEWS AND COMMENTS

Foundations of Plant Geography. By STANLEY A. CAIN. New York and London: Harper and Brothers, 1944: i–xiv, 1–556, figs. 1–63. $5.00.

As EDGAR ANDERSON has wisely said, Cain has brought together the stones but has not built them into a foundation on which a superstructure can be laid. Biogeography remains a mass of largely unorganized material. Perhaps some master mind can synthesize the fundamentals of a science of the geography of organisms. More likely, however, this accomplishment will evolve from the labors of many workers, a few of whom will contribute important constructive suggestions. Cain's compendium of facts and interpretations will render these labors easier and more likely to lead to synthesis. Its breath will go far toward making biologists in general biogeographically conscious. As a result more workers in more fields will consider the geographical implications of their findings, and will be more apt to publish such considerations either in a general section of their papers or in separate articles.

The science that should develop out of these distributional considerations will, it is hoped, be that of biogeography. Cain has obviously appreciated this need, for many of the examples that he gives are drawn from animal geography. Like genetics and evolution, biogeography should be a science bracketing the entire field of biology.

The variety of poorly synthesized fields that are basic to biogeography renders this a difficult book to review.

This difficulty is enhanced by a text that at times grows heavy, by some inconsistences in organization, and particularly by the ecologists' bad habit of using an unfamiliar jargon that is both literally and figuratively "Greek" to most biologists.   One may wonder whether ecologists may not be glossing over a deficiency of fundamental contributions by a veneer of highly technical terms.   The new term "areography" may be objected to not only for its novelty and its similarity to aerography, but also because it is of bastard origin and denotes a concept that is sufficiently well designated by "biogeography" and by "chorology."

Paleoecology appropriately is the first of four headings under which the "foundations of plant geography" are treated.   Why the chorological aspects of paleontology are not included as such is not evident.   Certainly the past distribution of organisms in space even when empirically determined, has a bearing on present distributions.   Such data are of course considered by Cain.   He probably adopted the section heading of paleoecology because he himself is primarily an ecologist and because he wanted to emphasize the important biogeographical bearings of this new phase of paleontology.   In this aim he was successful.   The presentation of paleoecological data and interpretations constitutes perhaps the most useful feature of the book for students of biogeography and speciation.   For instance, we have here what I understand to be the best summary of Mason's important researches on the Cenozoic history of the Californian closed-cone pines.   "Pollen Analysis as a Paleoecological Research Method" is another very informative chapter.

The main body of phytogeographic data are marshalled under "Areography."   Most of the interpretations in this section are characterized by a judicious objectivity rather than by a taking of sides on debated questions. For instance, in dealing with the controversy of whether primitive forms occur at the center or at the periphery of the range, his attitude is conservative and I think wise,

for logic as well as facts confirm his view that such forms
may now occupy either position, or neither.   Abundance
of forms is not taken as an invariable or reliable index of
center of origin, for "a phyletic stock that has had its
center of origin elsewhere may, through migration, en-
counter a region in which there are numerous available
ecological niches that are unsaturated, that is, in which
competition pressure is low.   Such a region may provide
a variety of habitats with at least partial isolation.
Under such conditions a phyletic stock may show a
'burst' of evolutionary adaptation."   That has the ring
of sound speciational philosophy.

As exemplified by this quotation there is much discus-
sion of speciation in the section on "areography" but the
main treatment of the species problem is given under the
third heading, "Evolution and Plant Geography."   Here
also is the discussion of such topics as isolation, species
stability and rate of evolution.   It is concluded that
speciation may be very rapid or very slow.

A single genetic aspect of the species problem, namely
polyploidy, is selected as the fourth and final section.
Unhappily, there is no concluding or summarizing section.

One of the main reasons why this treatise will stand
in many working libraries on the shelves allotted to often-
used books is the bibliography of 720 cited references : an
ample evidence of the long and devoted scientific labor
that went into the production of this outstandingly use-
ful volume.

Notices of New Books

Fact and Fiction in Modern Science. By Henry V. Gill.
First American Edition.   New York : Fordham University Press,
1944 : 1–136. $2.50.—Originally published in 1939 in Eire, where
it has gone through three printings, this series of essays by a
scientifically trained Jesuit priest is now offered to the American
public.   Repeatedly throughout the book there is inserted a
defense of the Catholic viewpoint.   I hope that intelligent
Catholic opinion is as broad as it is here said to be.   In regard
to evolution the opposition of the Church is indicated as being

limited to its denial of the view that life could have originated through the action of natural physical laws. The increased organization that is inherent in evolution is held to violate the basic physical law of entropy. A vital principle is therefore indicated, the author argues, and the existence of God is proved. The question of what part of human evolution is attributable to natural laws is avoided. As would be expected, birth control and eugenics through sterilization are opposed. In examining such treatises many scientists not steeped in Catholic doctrine will be struck by the inconsistency between a real scientific approach toward most problems and the inflexible conviction that certain documents and agencies are infallible, even when the claim for infallibility is restricted to a minimum of philosophical fundamentals and to certain applications of science to human affairs.

A Shorter History of Science. By WILLIAM CECIL DAMPIER. Cambridge: At the University Press; New York: The Macmillan Co., 1944: i–x, 1–189, pls. 1–9, figs. 1–14. $2.00.—The author of the great "A History of Science" has done science a new service in rewriting his major treatise in abbreviated and somewhat popularized form to make more widely available the fundamentals of this important subject. Modern science is clearly portrayed as an immense field, potent in its bearing on all phases of human culture. The accompanying plates are unfortunately drab, for they are printed on soft text paper. It is to be hoped that a more attractive edition will be produced when wartime restrictions permit.

The Book of Naturalists. An Anthology of the Best Natural History. By WILLIAM BEEBE. New York: Alfred A. Knopf, 1944: i–xiv, 1–500. $3.50.—An accomplished naturalist as well as an able writer, William Beebe was particularly well qualified to select and to annotate the material for this anthology. The selections are good and the annotations are illuminating, though, of course, others would have made different selections and might have prepared more detailed annotations. It is very doubtful, however, whether any one else would have compiled and condensed the gems of natural history writing of all time into a volume more likely to attract and hold the interest of general readers. Classical and foreign-language essays are presented in good English translations. Part I presents the production

of early naturalists, from an "unknown Magdalenian" cave painter, Aristotle and Pliny down to Thoreau. The second part samples modern natural history writings, from Darwin, Wallace, Agassiz and Huxley to Rachel Corson.

That Vanishing Eden: A Naturalist's Florida. By Thomas Barbour. Boston: Little, Brown & Co., An Atlantic Monthly Press Book, 1944: i–x, 1–250, 15 pls. $3.00.—As a source of pure intellectual joy there is almost no match for the experiences of a master field naturalist in an unspoiled land, rich in wildlife; for depths of regret there is little to equal the feelings of such a naturalist on the rapid despoliation of a land and biota that he has studied and loved. These joys and these regrets, vividly portrayed, are the theme of this altogether fascinating sequel to "A Naturalist at Large." The book appropriately starts with "The First to Arrive": the Miocene, Pliocene and Pleistocene Faunas, in the reconstruction of which the author has played a leading hand. Primordial Florida is then pictured through the highly regarded observations of William Bartram. Earlier human occupation is hinted at in the chapter on mounds. There is then given a sympathetic account of the Seminoles, which has been criticized as indicating a too complete loss of the aboriginal culture of these Indians. A very few other errors, excusable in the light of the tremendously broad and generally accurate nature wisdom of the author, were noted—for example, the statement that *Leptolucania ommata,* one of the oviparous cyprinodonts, is viviparous. Successive chapters deal with the Florida forests and the dire part that fires have played in their destruction; with delightful camping experiences; with beaches and sponges, springs and lakes, and mammals; with ditches, nature-destroying though often filled with a concentration of aquatic life; with "The Garden of Eden," alligators and crocodiles, the islands and the keys. The reader is then escorted to the "kampong" of David Fairchild, another grand naturalist whose world-wide wanderings have become increasingly confined to Florida, and to the Fairchild Tropical Garden. Final chapters deal with the Everglades National Park and with the future of Florida wildlife. The latter part of the book is written in a note of subdued optimism, as the author hopefully points out means by which the vast remaining natural history resources of our most nearly tropical state may be salvaged and utilized.

The Conservation of Natural Resources. A textbook for Junior and Senior High Schools. By H. BASIL WALES AND H. O. LATHROP. Chicago: Laurel Book Co., 1944: i–viii, 1–554, 191 figs., 5 maps, 7 charts. $2.00.—There are few needs so fundamental to our national future as is early and proper instruction in conservation. The lack of suitable texts has long deterred the filling of this need. For this reason the publication of this excellent book is an event of great potential importance.

In general the text is appropriately written down for senior high schools, though perhaps hardly for junior high schools. It should be suitable also for a non-professional college course in conservation. The authors have judiciously selected and balanced the material, though what P. S. Lovejoy termed the sawlog point of view is perhaps overstressed. Many preservationists and lovers of nature will flush over the suggestion "that the waste of timber in natural parks cannot be tolerated."

Such fundamentals as forestry, soil conservation and wise water utilization are particularly well treated, and it is a happy thought that this book may help to bring about a wiser public opinion and a stronger pressure for sane land management. Other phases of conservation are well covered; none of importance, except human conservation, is left out.

The factual basis is unusually sound, though statistical data are largely avoided. In parts perhaps too much detail is included for the purposes of a high school text. Inadequate and erroneous statements seem few, though not wholly lacking. Thus the suggestion that the depletion of fish in the Great Lakes has not been as serious as in smaller waters gives a very poor idea of the seriousness of the depletion of commercial fishes in the inland seas. Fishery workers will also be surprised at the statement that the marine and salmon fisheries are regulated by the federal Fish and Wildlife Service. Such minor inadequacies and errors could readily be eliminated in future editions. They do not deter us from saying, Well done, Wales and Lathrop.

Aquatic Plants of the United States. By WALTER CONRAD MUENSCHER. Handbooks of American Natural History, 4. Ithaca, New York: Comstock Publishing Co., 1944: i–x, 1–374, figs. 1–154, maps 1–400. $5.00.—As is characteristic of the Comstock publications, this new handbook is authoritatively written, thorough in scope, an important contribution to science as well

as to education. It is primarily a manual for the specific identification of the submersed and emersed aquatic plants of the fresh, brackish and marine waters of the entire United States. For this purpose the impressively clear-cut line drawings and the simple keys will serve well; often, however, only when flowers or fruits are at hand. The special emphasis on seeds and seedlings is an important feature. Two main criticisms occur to the reviewer. Firstly, the general introduction is tantalizingly curtailed. Secondly, the distributional maps, though a highly commendable feature, are not as instructive nor as neat as they might be. The major aquatic environments are poorly represented: less than a dozen each of lakes and streams are shown. With few exceptions there is given only a single record for any one state, and the placement of the dot is not consistently either the point of collection or the state center. The variable size and shape of the dots somewhat mars an otherwise very attractive presentation. These are, of course, minor criticisms. Muenscher has provided a very fine and useful handbook.

Birds of the Southwest Pacific. A Field Guide to the Birds of the Area between Samoa, New Caledonia and Micronesia. By ERNST MAYR. New York: The Macmillan Co., 1945: i–xix, 1–316, col. pls. 1–3, figs. 1–16. $3.75.—One of the minor tragedies of the Pacific operations has been the generally unanswerable call of zoology students in the war service for literature on the groups of animals in which they are interested. Their experiences would have been much richer, their life happier and their chance of making scientific observations or collections brighter, had books on the natural history of the region been available. For one group in one area, the birds of the Southwest Pacific, this need has now been filled, somewhat belatedly it is true. It is fortunate that the outstanding authority in the field has prepared this attractive book, which is well designed to meet the needs of the war-engrossed naturalist traveler.

Wildwood Wisdom. By ELLSWORTH JAEGER. New York: The Macmillan Co., 1945: i–xix, 1–491, pls. 1–193 and other figs. $2.95.—This "veritable encyclopedia of woods lore" is based largely on the expert woodcraft of American aborigines and early explorers but is made applicable to the needs of present-day

wilderness travelers. As the product of a long historical study of Indian lore, supplemented by frequent periods of living among the natives and by close contact with leading naturalists and outdoorsmen, it portrays the means of comfortable existence while living off the country in north woods, arctic and desert, without recourse to "the myriad jingle-jangle gadgets of some of our modern outdoorsmen." Hundreds of items of woods lore and of woodcraft are ably illustrated by the author's own clear and clever sketches.

The Problem of the Derivation of the South American and African Fresh-water Fish Faunas. By WILLIAM A. GOSLINE. An. Acad. Bras. Ciencias, 16, 1944: 211–223.—Following a brief statement of diverse theories that would explain the similar biotas of South America and Africa and a critique of the ichthyological evidence, Gosline concludes that "the routes by which the Ostariophysi [the chief group of fresh-water fishes] of the southern continents became distributed cannot at present be profitably discussed. I hope the point is equally clear, however, that ostariophysine distribution does not fit the mammalian dispersal pattern." He then points out promising lines of further investigation. Such avoidance of convictions is more frequent in theory than in practice.

Boletim do Museu Nacional, Rio de Janeiro, Nova Serie, Zoologia.—The separate numbers of the new series of zoological papers issued by the Rio museum are appearing at gratifying frequent intervals. Numbers 13 through at least 29 were published during 1944. Among these papers particular mention may be made of two by BERTHA LUTZ on the biology and embryology of anurans. One (No. 15) deals with the direct development of an *Eleutherodactylus*. A larger publication (No. 17) treats the "Biologia e taxonomia de *Zachaenus parvulus*." In Bulletin No. 24 AUGUSTO RUSCHI describes an intergeneric natural hybrid in the hummingbird family (Trochilidae).

SHORTER ARTICLES AND DISCUSSION

THE PRIMARY SEX RATIO IN DOMESTIC CHICKENS[1]

INTRODUCTION

So far as the writer is aware the primary sex ratio (percentage of males at fertilization) has not been reported for the domestic chicken. Mayr (1939) has reviewed the sex ratio in wild birds as far as known. It appears that there is a marked tendency for many species to produce an excess of one sex, usually the male.

Landauer and Landauer (1931) summarized the data on chicks from a large number of workers on the secondary sex ratio (per cent. of males at hatching). These data include 67,993 chicks, of which 48.77 per cent. were males. Crew (1938) found no significant differences in the sexes with respect to embryonic mortality rate. Crew also reports the secondary sex ratio on 515,976 sex-linked chicks hatched as 50.34. On 2,216,051 pure-bred and crossbred chicks where sex was determined by the Japanese method the sex ratio was 51.38. The secondary sex ratio appeared to differ with the breeds studied. Landauer and Landauer (1931) are inclined to believe that the embryonic mortality rate is slightly greater in males than in females, although they recognize that data so far reported are conflicting.

THE PRIMARY SEX RATIO

In order to discover the primary sex ratio in the domestic chicken it is necessary to select females that show 100 per cent. fertility and 100 per cent. hatchabality and to accurately determine the sex of all chicks hatched. The period of observation may logically extend through March and April, which is the normal hatching period in this locality. The objective is to determine the sex of the chick from every egg laid.

In the ten-year period from 1935 to 1944 a total of 39 pure-bred Rhode Island Red females mated to pure-bred Rhode Island Red males qualified for study. Each female had a perfect record in fertility and hatchability and produced ten or more chicks during March and April. Since the sex of chicks was not determined until the age of eight weeks, there was a loss of 61 chicks upon which no sex record is available.

In Table 1 data are presented in summary form.

TABLE 1

SEX RATIOS OF HATCHED CHICKS

Year hatched	No. of dams	No. of chicks		Sex ratio	Sex not determined
		Male	Female		
1944	8	70	78	47.3	9
1943	4	43	45	48.8	9
1942	0	none		. . .	. .
1941	4	51	47	52.0	3
1940	6	92	85	52.6	5
1939	5	50	48	51.0	10
1938	3	29	28	50.8	3
1937	2	22	22	50.0	4
1936	3	21	34	38.2	14
1935	4	54	51	51.4	4
Totals	39	432	438		61

In Table 1 the sex ratio of the 870 chicks whose sex was known was 49.7. In 1936 the sex ratio deviated widely from equality probably because of the large number whose sex was not recorded. By using the constant .527 recorded by Landauer and Landauer (1931) as the sex ratio of chicks dying between hatching day and eight weeks of age, it is possible to approximate the sex ratio of our total chick population. Simple calculation will add 32 males and 29 females to the totals in Table 1. The calculated grand totals became 464 males to 467 females which is as close to a 50 per cent. ratio as could be expected.

When only the 870 chicks whose sex is known are considered the sex ratio is 49.7. The standard error of mean difference between the yearly sex ratios and a 50–50 ratio was $\pm$ 1.42. These data again indicate that the primary sex ratio in Rhode Island Reds is 50–50.

In our data there were eleven hens with complete records for

TABLE 2

SEX RATIO OF CHICKS FROM INDIVIDUAL HENS

Hen No.	Chicks produced		Sex ratio
	Male	Female	
X296	4	14	22.2
X2670	4	7	36.4
T507	13	7	65.0
S2203	15	13	53.6
T2"52	18	12	60.0
S1042	9	9	50.0
R708	14	19	42.4
R1092	9	6	60.0
N2246	11	9	55.0
N2394	15	12	55.6
O2340	15	18	45.5
Totals	127	126	

sex of chicks produced.   These are presented in Table 2 to show the extreme variability in individual families.

The data in Table 2 show that great variability occurs in the primary sex ratio between different families.   This variability may be ultimately traced to gene differences.   It is not at all unlikely that sex in domestic chickens may depend upon many genes and that many of these are located in the autosomes.

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INDUCED PARTHENOCARPY IN GINKGO[1]

THE occurrence of apomixis in its various forms is fairly common among the angiosperms, but so far as is known, is unreported among the gymnosperms.   In some species of the angiosperms, apomixis is the usual method of embryo development and is genetically controlled, whereas in some other species, it appears to be facultative in the sense that it occasionally occurs normally in the failure of normal fertilization or it can be induced by various external stimuli such as x-rays, foreign pollen, chemicals, inadequate pollination, traumatic shock, etc.   These facultative apomicts may be either haploid or diploid, depending upon the process involved in the initiation of embryo development.

From *a priori* considerations, the induction of parthenogenesis in the gymnosperms, especially by the use of foreign pollen, has always appeared to the writer as more likely of success than among the angiosperms where extensive stylar tissue is such a barrier.   It is deemed relevant to here report the inadequacy of at least one *a priori* consideration.   In none of the gymnosperms pollinated with a variety of foreign pollens over a four-year period, has there resulted a single case of parthenocarpy save in Ginkgo.

The Ginkgo concerned is a female tree growing in the Coker Arboretum at the University of North Carolina.   There are no

male trees in the arboretum, nor in the vicinity of the campus known to the author. The tree has never produced fruit save when pollinated with Ginkgo pollen in 1941.

On April 7, 1943, pollen from *Cedrus deodara* (Roxb.) Loud, was liberally applied by broadcasting from near the top of the tree. The ovules were receptive as evidenced by the presence of a drop of mucilaginous exudate just outside the micropyle. As is well known, unpollinated ovules of Ginkgo soon die and drop from the branches. However, many ovules, after pollination with Cedrus pollen, did not abort as usual but persisted and slowly increased in size for several weeks before dropping. Only four seeds in all were recovered at the end of the season. Of the four, two were markedly reduced in size, averaging about half the size of normal seeds. One of these was sacrificed for examination and it appeared normal in every respect save size. What appeared to be an embryo was also observed. The three remaining seeds, after winter layering in sand, were planted in the greenhouse in early March. The remaining small seed promptly died, but the two larger seeds cracked their coats and appeared to be growing. However, after three months in the greenhouse, one seed died after emerging from the seed coat and swelling considerably, but without having put forth either radicle or shoot. The remaining seed is still alive and in precisely the same stage of development.

In the absence of adequate somatic tissue for a chromosome count, it is not known whether these embryos, if present, were haploid or diploid, and for the same reason it is impossible to say just what apomictic mechanism was responsible for their development, although pseudogamy is certainly indicated. In view of the genetic and morphological gaps between Ginkgo and Cedrus, it seems safe to say that syngamy was not involved.

The experiment was repeated this spring, but an unseasonably late frost killed all ovules and nearly denuded the tree of leaves.

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THE YELLOW–ORANGE ENDOSPERM OF MAIZE[1,2]

THE genetics of the yellow-orange endosperm color in maize has been examined by several investigators. A discussion of the

[1] Preliminary note.

[2] Part of this work was done in the Genetics Department of the University of Missouri, on a fellowship of the Guggenheim Foundation.

pertinent literature will be given in another publication; suffice it to say here that two main genes with complementary effects, Y_1 and Y_3, are involved. These genes are located in chromosomes 6 and 2, respectively (Emerson, 1921; Perry and Sprague, 1936). Two other genes with effects similar to those of Y_1 have been reported: Y_2 in chromosome 5 (Eyster, 1931), and Y_4, linkage group unknown (Singleton).[3] Tests of Y_4 material received from Dr. Singleton indicate that Y_4 is identical with Y_1. The Y_2 stock is apparently lost. The location of this gene was made by examining its linkage with the gene vp_2 (vivipary or premature germination) (Eyster, 1931). Mangelsdorf (1926) described several genes for premature germination giving apparent linkage with yellow endosperm color, probably due to some physiological effect of premature germination on the pigmentation of the endosperm. It is possible that Y_2, like Y_4, is a synonym of Y_1.

The seed color in $Y_1 Y_3$ stocks may vary from a yellow similar in shade to that of a pale egg-yolk, to a deep orange found in South American maize and such strains of North American corn as Louisiana Yellow Creole Flint, which is probably of South American origin. As already reported by Andres (1939) and Sprague (personal communication), this variation is due to modifiers. The results obtained by us in crosses of South American deep orange strains with yellow North American ones are shown in Table 1.

Crosses of deep orange endosperm × white endosperm also show clearly the effects of modifiers on the $Y_1 Y_3$ basic condition. F_2 and F_3 ears and seeds show various shades of yellow and orange colors. However, by selection from this material it is, as shown in Table 2, possible to establish strains in which the difference orange *vs.* yellow behaves as if controlled by a single gene.

The location of this gene is as yet unknown. It will be examined in special experiments, but since the modifiers that may be present in tester stocks may obscure the segregation these experiments will take time.

A new gene complementary to Y_1, referred to below as Y_5, has been isolated from a cross of a deep orange Brazilian strain, "Cateto," with a tester strain $y_1 y_3$–*al* received from Argentina. The interaction of Y_1 and Y_5 produces a yellow endosperm color resembling that of a pale egg-yolk.

[3] W. R. Singleton, in Maize Genetics Cooperation, *News Letter*, March 4, 1936. Cited with permission of the author.

TABLE 1

F_2 OF DEEP ORANGE ENDOSPERM STRAINS OF SOUTH AMERICA WITH
YELLOW ENDOSPERM STRAINS OF NORTH AMERICA*

Pedigree (1942)	Deep orange		Orange		Yellow
832– 8	57	←———	99	———→	44
832– 1		←——— 144			89
832– 2			114	———→	100
833– 3		←——— 60		———→	71
833– 5			122	———→	41
833– 1		←——— 146	———→		
851– 6	58		48	———→	72
851– 9	31	←———	109	———→	55
851– 3	18	←———	84	———→	29
851– 2	85	←———	191	———→	71
851–10	34	←———	241	———→	59

(1942) Pedigree	Deep orange	Orange	Orange-yellow	Yellow-orange	Yellow
882–10	16	59	70	31	24
882– 3	15	77 ←———	..	———→ 59	11

* The arrows indicate the presence of intermediate classes not possible to classify.

Data demonstrating the existence of this gene and its interrelations with Y_1 and Y_3 are presented in Table 3. Linkage with Pl and al indicates the presence of Y_1 and Y_3 in the deep orange strain used. The gene y_3 is identical with or very closely linked to al (Perry and Sprague, 1936). The apparent crossovers shown in Table 3 proved to be due either to hetero-fertilization or to classification difficulties. Cytology of chromosome 2 in a y_3–al plant showed no sign of deficiencies that could be responsible for both the white seeds and the albescent seedlings effects. Of course, these effects may be produced by a deficiency so small as to be invisible; however, the transmission of this condition both through ♀ and through ♂ gametes is normal.

The plants designated $y_1 y_3$–al were received from Argentina; they have been isolated from crosses of North American tester with South American deep orange endosperm strains. The Y_3 gene present in the $y_1 y_3$–al tester was presumably introduced from South American material. That Y_3 is indeed a gene for

TABLE 2

SIMPLE SEGREGATION FOR ORANGE VS. YELLOW IN A SELFED LINE

Pedigree (1942)	Orange	Yellow	Deviation 3 : 1	X^2	P
951–4	156	54	1.50	0.06	0.80
951–3	142	62	10.00	2.56	0.11
951–1	208	59	– 7.75	1.19	0.29
Total	506	175	4.75	0.42	0.52

TABLE 3

INHERITANCE OF Y_5 AND INTERRELATIONS WITH Y_1 AND Y_3

I. F_2 Progeny 730-2 (1940). $\dfrac{Y_1\,pl}{y_1\,Pl}\ \dfrac{(Y_3\,Al)b}{(y_3\,al)B}\ \dfrac{Y_5}{Y_5}\ \dfrac{A}{a}$

Class	Genotypes	Seeds	Calculated 9 : 3 : 4	X^2	P
orange-yellow	Y_1–Y_3–Y_5	226	220.03	0.162	0.68
yellow	Y_1–$y_3\,Y_5$	71	74.01	0.122	0.72
white	$y_1\,Y_3$–Y_5	98	98.68	0.004	0.95
white	$y_1\,y_3\,Y_5$				

Class	Seeds germinated		Plants obtained		A–B–Pl–	A–b Pl–	A–B–pl	A–b pl	a
	Al	al	Al	al					
orange-yellow	169	4	159	0	57	9	31	8	54
yellow	0	46	0	7	3	4	0	0	0
white	60	..	56	..	30	8	3	4	11
white	..	14	..	4	4	0	0	0	0

Class	Observed		Calculated on 28% crossing-over Y_1–Pl		X^2		P	
	A Pl	A pl	A Pl	A pl	A Pl	A pl	A Pl	A–pl
orange-yellow	66	39	77.94	34.56	1.83	0.55	0.17	0.47
yellow	7	0	....	....	...	...	...	...
white	38	7	34.56	2.94	0.35	5.60	0.58	0.02
white	4	0	....	....	...	...	...	...

II. Backcross Progeny

730-9 × 770-7 (1940). $\dfrac{Y_1\,pl}{y_1\,Pl}\ \dfrac{(Y_3\,Al)b}{(y_3\,al)B}\ \dfrac{Y_5}{Y_5}\ \dfrac{A}{a} \times \dfrac{y_1\,pl}{y_1\,pl}\ \dfrac{(y_3\,al)B}{(y_3\,al)B}\ \dfrac{Y_5}{Y_5}\ \dfrac{A}{A}$

Class	Genotypes	Seeds	Calculated 1 : 1 : 2	X^2	P
orange-yellow	Y_1–Y_3–Y_5	87	84.75	0.059	0.80
yellow	Y_1–$y_3\,Y_5$	81	84.75	0.166	0.69
white	$y_1\,Y_3$–Y_5	171	169.50	0.013	0.90
white	$y_1\,y_3\,Y_5$				

Class	Seeds germinated		Plants obtained		Pl	pl
	Al	al	Al	al		
orange-yellow	77	9	67	0	18	49
yellow	2	72	0	0	0	0
white	83	..	83	..	69	14
white	..	85	..	24	21	3

Class	Observed		Calculated on 28% crossing-over Y_1–Pl		X^2		P	
	Pl	pl	Pl	pl	Pl	pl	Pl	pl
orange-yellow	18	49	21.0	54.0	0.43	0.46	0.52	0.50
yellow	0	0	...	...	...	...	...	...
white	69	14	54.0	21.0	4.16	2.33	0.03	0.13
white	21	3	...	...	...	...	...	...

endosperm color has been checked in the cross ♀ white endosperm $y_1\,y_1\,y_3\,y_3\,y_5\,y_5 \times$ ♂ yellow endosperm $Y_1\,y_1\,y_3\,y_3\,Y_5\,Y_5$, which gave about 50 per cent. of yellow and 50 per cent. of white seeds.

The new complementary gene gave, in extractions from a cross with Y_3, ratios of 36 yellow-orange: 9 yellow: 19 white ($Y_1 y_1 Y_3 y_3 Y_5 y_5$), and 9 yellow: 7 white ($Y_1 y_1 y_3 y_3 Y_5 y_5$). A ratio of 12 yellow-orange: 3 yellow: 1 white or 15 colored: 1 colorless ($Y_1 Y_1 Y_3 y_3 Y_5 y_5$), should also be expected. The relationships between the new gene and that producing similar ratios reported by Sprague[4] are not known.

The results obtained in back-crosses of $Y_1 y_1 Y_3 y_3 Y_5 Y_5$ to $Y_1 Y_1 Y_3 y_3 y_5 y_5$ are in accordance with expectations. Back-crosses of the same F_1 to $y_1 y_1 Y_3 Y_3 y_5 y_5$ gave the expected ratio 1 yellow-orange: 1 white when the F_1 was the ♀ parent. As ♂ parent on the $y_1 y_1 Y_3 Y_3 y_5 y_5$ tester the expected ratio 1 yellow-orange: 1 white was changed to approximately 1 yellow-orange: 3 white. Plants obtained from these seeds segregate normally according to the expectation on a $Y_1 Y_3$ basis and the F_1 pollen gave the expected 1:1 ratio on other $y_1 y_1 Y_3 Y_3 y_5 y_5$ stocks, indicating that we have to deal here with some kind of preferential segregation in favor of the y_1 gene in a particular ♀ genotype, similar to that found in pop-corn maize by Demerec (1929). This working hypothesis will be tested.

Deep orange endosperm strains crossed with several lines of white endosperm and with testers for all 10 chromosomes show segregation for only one yellow endosperm gene, Y_1 in chromosome 6. All testers and white endosperm strains crossed are $y_1 y_1 Y_3 Y_3$, and the interaction $Y_1 Y_5$ can be detected only in a $y_3 y_3$ genotype. The location of the Y_5 gene is therefore rather difficult, since all testers in our hands are Y_3 and unknown with respect to the Y_5 gene. The problem is difficult because it involves observing the segregation of three genes with cumulative effects or the endosperm color. Testers of $y_3 y_3$ constitution would simplify the matter, but unfortunately such plants grow very poorly (compare data in Table 3).

The deep orange endosperm strains of Brazil contain also a gene for yellow aleurone color located by proper tests in chromosome 7, and probably an allele of Bn_1 (Kavakan, 1924). The $Y_1 Y_3 Y_5$ genes and other modifiers of the $Y_1 Y_3$ control the carotenoid pigments, the color of the seeds varying from yellow to deep orange. The yellow aleurone gene, as reported already by Kvakan (1924) controls the yellow pigment only in the

4 G. F. Sprague, in Maize Genetics Cooperation, *News Letter*, March 6, 1938. Cited with permission of the author.

aleurone layer. These seeds are of a *lemon-yellow* color and are different from the yellow-orange seeds. The genetics of the yellow aleurone is independent from that of yellow endosperm, and the Bn_1 gene is also affected by modifiers. It is present in several strains of corn, making the analysis of the yellow-orange endosperm sometimes difficult.

The carotenoid pigments in plants of different genotypes are being analyzed. The results so far obtained are in accordance with those of other authors (Mangelsdorf and Fraps, 1931; Randolph and Hand, 1940). Biological tests of the same material will be carried on in collaboration with the Physiological Department of the Medical School, University of Sao Paulo.

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